Assembly patterns of mammal communities in a restored fragmented agroecosystem

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Assembly patterns of mammal communities in a restored fragmented agroecosystem

Memoria presentada por el Licenciado Bruno David Suárez de Tangil Suárez para optar al título de Doctor por la Universidad Pablo de Olavide

Director: Alejandro Rodríguez Blanco

Estación Biológica de Doñana -

Consejo Superior de Investigaciones Científicas

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CERTIFICA

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral "Assembly patterns of mammal communities in a restored fragmented agroecosystem" son aptos para ser presentados por el Licenciado en Biología Bruno David Suárez de Tangil Suárez ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad Pablo de Olavide.

Y para que así conste, y en cumplimiento de las disposiciones legales vigentes, extiendo el presente certificado a 30 de abril de 2018.

Firma Director:

Dr. Alejandro Rodríguez Blanco

"*If a tree falls in a forest*

and no one is around to hear it,

does it make a sound?"

George Berkeley

(1685-1753)

Contents

1. Introduction

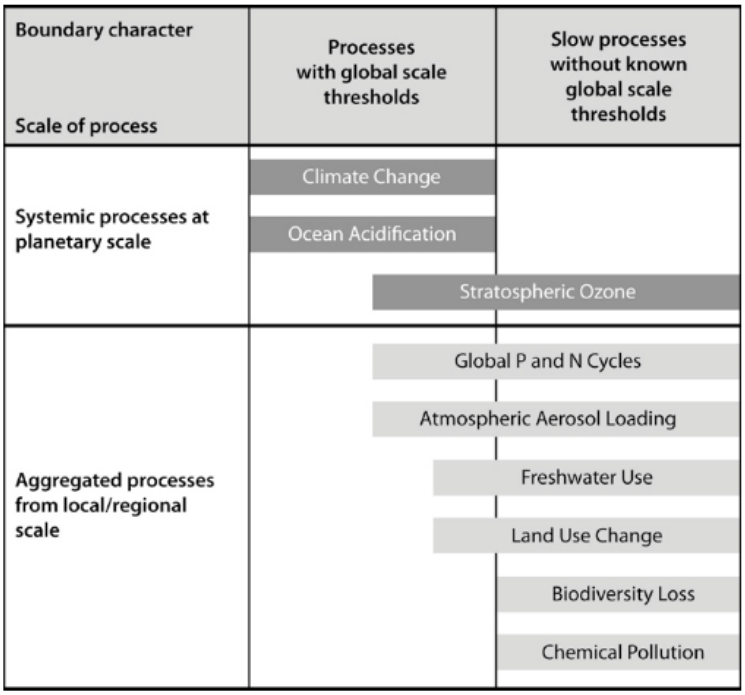
The human population has been grown at an exponential rate since the start of the industrial revolution in the early 1700s (Goldewijk 2005) and the demand for agricultural land has increased at a similar rate. As a consequence, the scarcity of fertile land is becoming one of the main challenges to overcome (Godfray et al. 2010; Fischer et al. 2014). A global net forest loss of 1.5 million square kilometres has been documented in the last years (Hansen et al. 2013). In 2000, 34% of Earth's surface was covered by croplands and pastures (Ramankutty et al. 2008); and following the projections of the Food and Agriculture Organization of the United Nations, FAO, we expect an expansion of the global agricultural area from the current 5.1 billion ha to 5.4 billion ha in 2030 (Wirsenius et al. 2010). However, there is an important variation between the so-called developed and developing countries (Balmford et al. 2005). In developed countries, cropland areas are expected to decrease (Balmford et al. 2005), whereas in developing countries, due to the faster human population growth, cropland areas are expected to increase (Miao et al. 2013; Schmitz et al. 2014).

To deal with future food demand farm yields must reach, on average, 70-80% of the yield potential (Cassman 1999), especially in developing countries. In Asia, commercial and extensive farms are expanding, and the intensification of agricultural landscapes is increasing to the detriment of small farms devoted to subsistence production (Pingali 1997). In South America, substitution of the traditional extensive agriculture by an intensively managed agriculture has also been reported (Dias et al. 2016). However, adopting an intensive cultivation scheme does not preclude cropland expansion, depending on the quality and type of governance (Graziano Ceddia et al. 2014), and patterns of people migration and settlement in close or distant marginal lads (Barretto et al. 2013; Kalamandeen et al. 2018).

Biogeochemical nitrogen and phosphorus cycles, global freshwater use, land system change and biodiversity loss, which are often associated with the intensification of agricultural landscapes (Foley et al. 2005; Stoate et al. 2009; Chappell and LaValle 2011; Hosonuma et al. 2012; Baudron and Giller 2014), have been identified as planetary boundaries (Figure I1; Rockström et al. 2009).

The transgression of one or more of these planetary boundaries may compromise global sustainability. Nevertheless, it is estimated that two of these boundaries, the biogeochemical nitrogen cycle and the biodiversity loss, have already been transgressed (Rockström et al. 2009; Newbold et al. 2016; Campbell et al. 2017). Hence, one of the main challenges for humanity in the next years will be to reach high yield farming without causing deep environmental damages (Rockström et al. 2017) and conservation conflicts (Dobrovolski et al. 2011).

Figure I1 Categories of planetary boundaries (drawn from Rockström et al. 2009).

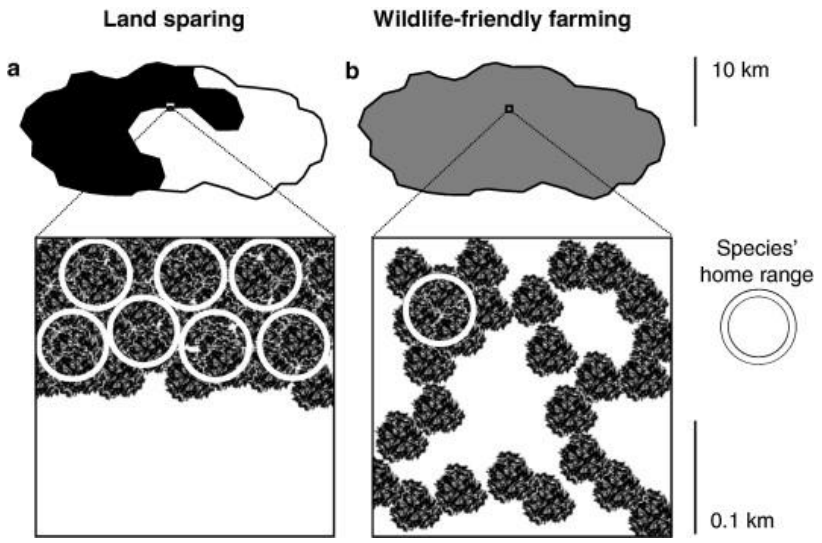


Models accounting for the economic activity, agricultural production and biodiversity loss predict a global expansion of the intensively managed croplands and an increase in the number of species threatened (Lenzen et al. 2013). Multiple examples of the negative influence of intensively managed agricultural lands on biodiversity have been reported. These effects can be directly caused by the land use intensification, by factors indirectly associated with agricultural intensification, or simultaneously by both direct and indirect factors. One example of direct effect was described by Attwood et al. (2008), who found that global arthropod richness was significantly higher in areas with less intensive land use. Indirect effects were illustrated by Gibbs et al. (2009), who described the negative effect of pesticides use in intensive agricultural landscapes on imperiled species. Righetto Cassano et al. (2014) found both direct (decrease of forest cover and connectivity) and indirect negative effects (increase in the density or activity of domestic dogs on mammal diversity).

However, several actions have been proposed to meet world's future food security without aggravating agriculture's environmental footprint (Kearney 2010; Foley et al. 2011; Beddington et al. 2012). Again, one of the most important actions involves increasing crop efficiency without increasing cropland area (Phalan et al. 2011b).

Therefore, harmonising biodiversity conservation and competing demands for land exploitation is one of the current challenges for conservation biologists (Lambin and Meyfroidt 2011). Two main conservation strategies have been proposed and widely discussed: land sparing and land sharing (Figure I2). The land sparing strategy allocates some land for conservation (i. e. nature reserves), and allows intensive exploitation elsewhere. On the contrary, the land sharing strategy promotes maximising biodiversity in agricultural land. Several studies have pointed out that land sparing strategy is more effective for biodiversity conservation than land sharing strategy (Green et al. 2005; Caryl et al. 2016; Phalan et al. 2016), even for isolated nature reserves surrounded by very hostile

Figure I2 Two land use scenarios representing a) land sparing, and b) land sharing conservation strategies at two different spatial scales (Phalan et al. 2011a). In scenario (a) the area is divided between a protected forest landscape (black) and a high-yield farming landscape with no forested patches (white). In scenario (b) the entire area is allocated to small forested patches embedded in a lower yield wildlife-friendly farming landscape (grey). The white circles represent the minimum contiguous area required to support the home range of a forest species intolerant to transformed habitat. The yield per unit area of the farming landscape is lower applying wildlife-friendly farming because of the remaining unproductive forest patches, but biodiversity is expected to increase compared to intensive farming.



land uses (Gilroy et al. 2014). The land sparing strategy may fail when the size of protected areas is small, which, in many cases, is the only option available (Maiorano et al. 2008). Land sparing can reduce the probability of persistence of open-habitat species in agricultural landscapes (Wright et al. 2012) and does not guarantee the total integrity of ecological communities within nature reserves due to edge effects (Lamb et al. 2016). Likewise, land sparing does not prevent the collection of tree products from "spared" forests, which can impact forest

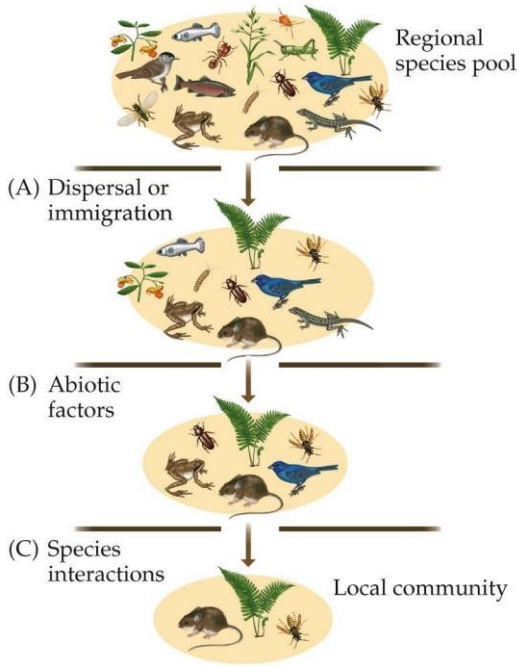
conservation when agricultural intensification is promoted (Quandt 2016). Finally, high-yield farming affects not only the portion of land dedicated to farming but also regions downwind or downstream of intensively managed areas (Matson and Vitousek 2006).

To avoid insufficient protection for natural habitats, other ecosystem services and social welfare, agricultural policies should be better integrated for combining land-use planning and technical support for small farmers (Hulme et al. 2013; Dotta et al. 2016; Tilman et al. 2017). Thus, wildlife-friendly farming and land sparing used together, as part of an integrated approach, can offer complementary benefits to biodiversity conservation (Troupin and Carmel 2014; Kremen 2015; Gálvez et al. 2018). Specific policy guidelines for agricultural landscapes may depend on particular agroecosystem characteristics (Fischer et al. 2008), and conservation science has a key role to understand and effectively manage agricultural landscapes (Norris 2008).

Nowadays, it is widely accepted that local ecological communities are influenced by a combination of local and regional processes (Figure I3; Ricklefs and Schluter 1993; Ernest et al. 2008; Logue et al. 2011). The focus is now on understanding the relative importance of those processes on metacommunity structure (Moritz et al. 2013). This reinterpretation of community ecology theory within a metacommunity framework is described by four major theories: patch dynamics, species sorting, mass effects and the neutral model (Leibold et al. 2004; Holyoak et al. 2005; Moritz et al. 2013). Species occurrence under patch dynamics responds to a balance between local colonisation and extinction (Leibold et al. 2004). Species sorting is determined by niche requirements (Cottenie 2005). Mass effects emphasise that dispersal overcomes niche requirements, and species occurrence is possible even under *a priori* unsuitable environmental conditions (Mouquet and Loreau 2003). Lastly, the neutral model by Hubbell (2001) describes random fluctuations in community composition. It has been suggested that researchers should focus less on classifying metacommunities into one of those ecological theories, and more on studying the relationship

between dispersal and environmental signals and their effect on the metacommunity structure (Winegardner et al. 2012).

Figure I3 Hierarchical representation of ecological filters affecting the structure of local communities after Cain et al. (2014). Species dispersal from regional species pool establishes the first ecological filter. Species tolerance to local abiotic conditions set the second ecological filter. Finally, interspecific interactions also determine an ecological filter for local communities.



Habitat loss and fragmentation can shape ecological communities, favouring generalist over specialist species (Fahrig 2003; Miller et al. 2015), impoverishing species assemblages (Devictor and Jiguet 2007; Chisté et al. 2018), and impairing ecological functions (Magioli et al. 2015). Island biogeography theory

(MacArthur and Wilson 1963; Losos et al. 2010) and metapopulation theory (Hanski 1999) were adopted as a framework for studying biodiversity in fragmented landscapes such as agroecosystems. These theories predict that more isolated and smaller fragments are less likely to receive immigrants from other fragments and might face higher extinction rates due to stochastic events (Figure I4, I5). Local extinctions are highly related to the amount and quality of resources in the habitat fragment (Hanski 1998). However, key factors at the landscape level such as "edge effects" or the influence of the surrounding matrix, have revealed some limitations of the metapopulation theory (Laurance 2008). The composition of the surrounding landscape also influences dispersal between habitat fragments (Prugh et al. 2008), increasing (Martensen et al. 2008) or decreasing (Uezu and Metzger 2011) fragment (re)colonization rates (Revilla et al. 2004) or rescue effects (Brown and Kodric-Brown 1977), and then influencing the colonization-extinction dynamics in the fragments (Borges-Matos et al. 2016).

The process of dispersal can be divided into three stages: emigration from habitat patch, transience through non-habitat or resource-poor habitat patches, and settlement (Baguette et al. 2013). These stages are defined by the risks and benefits experienced by the individual (Bonte et al. 2012). In agroecosystems, landscape heterogeneity affects movement because different habitats present different levels of risk and benefit (Driscoll et al. 2013). The matrix structure can enhance movement between habitat fragments (Prevedello and Vieira 2010). However, "fence effects" (Schtickzelle and Baguette 2003), altered behaviour (Cibot et al. 2015) or increased mortality (Vickers et al. 2015) can diminish movement between fragments. Therefore, colonization probability is not only a matter of distance but it might also depend on the permeability of the different matrix types to animal movement. Thus, colonization-extinction dynamics depend on landscape connectivity (Fischer and Lindenmayer 2007), or the degree to which landscape structure affects the movement of organisms between habitat fragments (Ricketts 2001; Poniatowski et al. 2016).

Figure I4 The equilibrium (island biogeography) model proposed by MacArthur and Wilson (1963) to explain the number of species in oceanic islands. Isolated and smaller islands are less likely to receive immigrants from the mainland and might face higher extinction rates due to stochastic events. Less isolated islands are more likely to receive colonists from the mainland and, the probability of colonization of large islands will be higher than that of small islands.

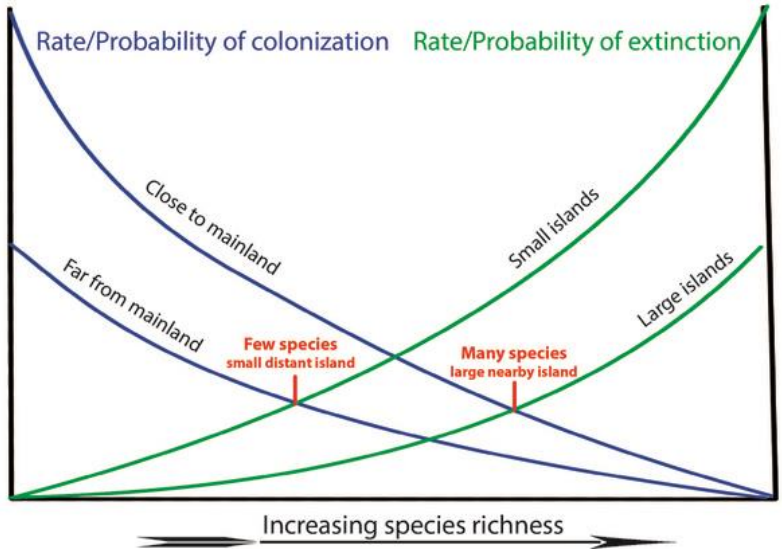
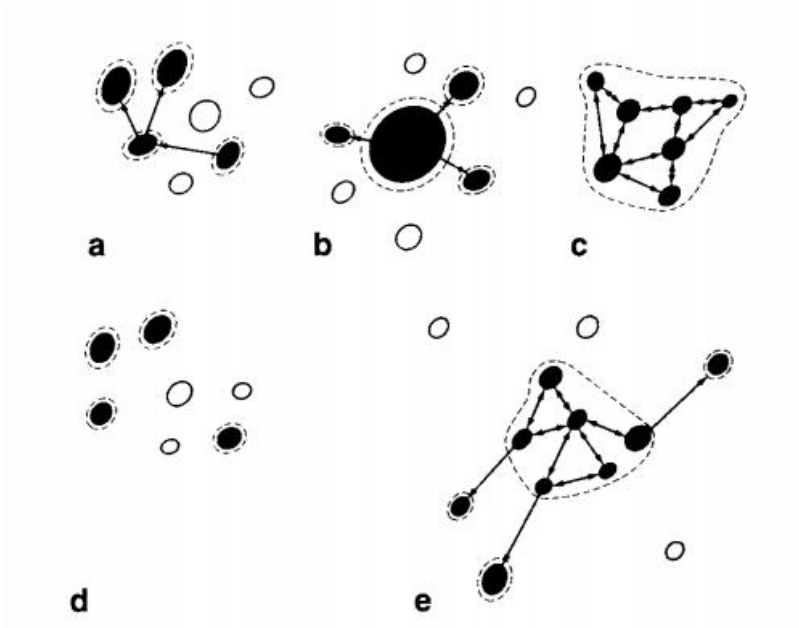


Figure I.5 Different types of metapopulation models (Harrison and Taylor 1997). Filled circles represent occupied habitat patches; empty circles are vacant habitat patches; dotted lines delimit boundaries of local populations and arrows represent dispersal. Metapopulation models are a) classic (Levins 1969); (b) mainland-island (MacArthur and Wilson 1963); (c) patchy population; (d) non-equilibrium metapopulation; and (e) intermediate case combining features of a, b, c, and d.



The conservation of ecological communities in agricultural landscapes should alleviate the effects of fragmentation by increasing landscape connectivity. A way to increase connectivity between fragments in transformed agricultural landscapes is the restoration of small patches acting as stepping stones that would link otherwise isolated patches (Uezu et al. 2008; Kramer-Schadt et al. 2011; Saura et al. 2014). Another strategy is the establishment of natural physical continuous corridors between forested fragments (Crespin and García-Villalta 2014; Ramiadantsoa et al. 2015). The effectiveness of these strategies

depends on the surrounding matrix: higher effectiveness is likely to be achieved in low-resistance matrices, whereas low rates of inter-fragment dispersal are expected in high-resistance matrices (Baum et al. 2004).

Mediterranean ecosystems have suffered landscape homogenisation as a consequence of an increase in forest cover in abandoned fields, a decrease in the proportion of farmland areas, and an intensification of herbaceous crops on the coastal agricultural plains (Falcucci et al. 2007; Serra et al. 2008; Geri et al. 2010). In Europe, irrigated and extensive farmland areas are more frequent in the Mediterranean regions than in temperate or boreal regions, being Spain is one of the most vulnerable countries to biodiversity loss (Reidsma et al. 2006). Land use changes and cropland expansion have been reported in southwestern Spain since XV century, mainly lead by the cultivation of cereals, vineyards and olive groves in plain areas (Herrera-García 1980; Borrero-Fernández 1983; Delgado Bujalance 2004; Palomo et al. 2014).

Iberian mid-sized mammals consist of representative species of both the Maghreb (north-west Africa) and Iberia (south-west Europe) (Dobson 1998). Mammals in general, and carnivores in particular, are thought to be particularly vulnerable to local extinction in fragmented landscapes (Crooks 2002; Wiegand et al. 2005) because of their relatively large home ranges, low density, elusive and secretive behaviour, nocturnal activity, and direct persecution by humans (Kanagaraj et al. 2013; Farris et al. 2015; van der Meer 2018). These traits often compromise mammal detection (Vine et al. 2009), making direct observation quite difficult. Therefore, the identification of efficient non-invasive survey methods become particularly interesting for conservation planners and managers (Wright et al. 2014). Carnivores are involved in many ecological interactions with important functions at the community level. Examples are the cascading effects given their roles as predators (Malo et al. 1999; Díaz-Ruiz et al. 2013), herbivores (Rueda et al. 2008) or dispersers and predators of seeds (Fedriani and Delibes 2009; Virgós et al. 2010; Rico-Guzmán et al. 2012). Therefore, the negative effect of land use changes on Iberian carnivore guilds is expected to result in biodiversity loss.

General aim

The aim of this thesis is to understand the mechanisms driving the biodiversity loss associated with the agricultural intensification, which promotes the landscape simplification, homogenisation and impoverishment. Specifically, we examine the contribution of the structure, the quality and the function of the landscape elements using carnivores as a model group.

We first analyse the efficiency of olfactory, visual and acoustic lures in detecting mammal species throughout the agroecosystem. We then evaluate the effectiveness of passive and active survey methods in detecting mammals. We estimate carnivore connectivity routes between forest landscapes across the agroecosystem, identify critical connectivity sites and simulate the restoration of hedgerows to assess their effect on landscape connectivity. We also analyse the contribution of regional and local processes on species occupancy in fragments embedded in the agroecosystem and examine whether their contribution differs regarding agricultural landscape structure. Finally, we analyse the effect of regional and local processes on the variation in mesocarnivore species composition in the agroecosystem and the surrounding forest landscapes.

In the next pages, we describe the specific context, objectives and hypotheses of each of the investigations addressed in this thesis.

1.1 Detection of Iberian terrestrial mammals employing olfactory, visual and auditory attractants

Monitoring programmes are required to understand the effects of human activity on wildlife and to assess the effectiveness of remediation through conservation management. As human disturbance may alter whole landscapes and make many species vulnerable, its ecological consequences often need to be documented through large-scale multispecies monitoring (Manley et al. 2004; Watson and Novelly 2004; Wright et al. 2014; Karanth 2016).

Track stations and remote cameras are standard methods for surveying wild terrestrial mammals (Roberts et al. 2006; Long et al. 2008; Paull et al. 2012; Núñez-Regueiro et al. 2015). These passive methods of detection are typically used in combination with non-edible lures or edible baits. Lures are often deemed functional on the basis of the practitioner's impressions, as illustrated in the cases compiled by Novak et al. (1987). Most studies formally addressing lure functionality have confirmed that using attractants may actually increase the frequency of mammal detection (e. g., Chamberlain et al. 1999; Tanner and Zimmerman 2012; Stratman and Apker 2014). However, the possibility exists that a given lure attracts some species but not others. Understanding the response of multiple species to lures is essential to design protocols for monitoring mammal communities.

Most research on lure efficiency has pursued optimising attractants, and the way they are presented, for a particular species while trying to keep low visitation rates by non-target species. For example, high specificity of lures or baits is desirable to reduce the side effects of predator control (Travaini et al. 2001; Hughes et al. 2011), improve the efficiency of trapping or non-invasive collection of biological samples in single-species studies (Schmidt and Kowalczyk 2006; Barrett et al. 2008), or deliver vaccines or other substances in the management of zoonoses (Steelman et al. 1998; Jojola et al. 2007). In contrast, comparison and selection of lures to simultaneously monitor multiple mammal species have drawn less attention. The use of multiple species-specific attractants has been suggested to achieve this goal (Andelt and Woolley 1996; Schlexer 2008; Cove et al. 2014). However, in large-scale surveys, using a single, general-purpose lure able to detect most species might be easier, cost-effective and therefore preferable.

Designs employing several attractants often place a single lure per recording site (Ausband et al. 2011; Pederson et al. 2012; Hedges et al. 2015). However, assuming that mammals are attracted by different types of sensory cues, and their response to them may be additive, a combination of lures per site has also been used. Compounded lures that have been assessed include bait plus scent

(Hunt et al. 2007; Espartosa et al. 2011), bait plus visual (Warburton and Yockney 2009), or scent plus visual (Edwards et al. 1997), among others. Likewise, several types of auditory lures have been considered alone or in combination (Carey et al. 1997; Chamberlain et al. 1999; Ober et al. 2011). Using more than one lure requires extra time to set each station and to maintain or replace the lure in subsequent visits. Time and cost are important factors in the design of large-scale mammal surveys, and multiple lures in a single station should be adopted only if an actual improvement in detection efficiency is achieved as compared with single lure sets (Williams et al. 2011).

In monitoring programmes, variation in the frequency of detection should be attributed to changes in mammal occupancy or abundance rather than to variation in lure appeal, which ideally should be kept constant. However, the performance of lures may vary with environmental conditions. Diffusion of volatile substances present in olfactory attractants may be higher in warmer periods. Light, hanging visual attractants (Tanner and Zimmerman 2012) may be more evident in blowing breeze or wind, whereas shiny lures (Molsher 2001; Cove et al. 2014) would perform better under natural light. Visibility would also decrease with increasing vegetation cover.

Our aim was identifying a general-purpose lure suitable for large-scale surveys of terrestrial mammal communities in a Mediterranean environment. Henceforth, we restrict the meaning of lure to non-edible substances or objects that may draw the attention of mammal species, and use attractant as a synonym. For mammal species that are detectable with remote cameras and track stations, we assess whether 1) two widely used olfactory attractants differ in their ability to detect as many mammal species as possible, 2) adding visual and acoustic lures to olfactory attractants increases mammal detection rates, and 3) detection rates at sites with suspended lures decrease with low visibility, expressed as high woody cover, calm wind, and low levels of moonlight illumination.

1.2 Relative efficiency of different survey methods for detecting wild mammals

Wild mammals are often the target of conservation, exploitation or population control. To evaluate the effects of management practices on species distribution and abundance, monitoring requires effective techniques that maximise mammal detection (Lesmeister et al. 2015; Rayan and Linkie 2015). Many mammal species are not conspicuous, show elusive behaviours, are nocturnal, or need large areas to satisfy their ecological requirements. These traits make mammal detection through direct observation quite difficult. Under these circumstances, non-invasive survey methods become particularly appropriate for monitoring mammals (Long et al. 2008). Non-invasive survey methods are effective, relatively cheap and do not require that the animals be directly observed or handled (Thorn et al. 2010).

Scientific literature offers multiple examples of comparison of survey methods for detecting mammal species (Gompper et al. 2006; Long et al. 2007; Monterroso et al. 2014). Different methodologies typically show differences in detection success because of the presence of false negatives due to certain sampling conditions (Foresman and Pearson 1998; Lyra-Jorge et al. 2008; Olifiers et al. 2011). The use of just one detection method often does not provide a homogeneous or constant level of detection. Detection depends on time (fluctuations in animal behaviour; e. g., Villafuerte et al. 1993; Ruzicka and Conover 2011), ecological (habitat) and environmental (meteorological variables) features (Soto et al. 2012), and species-specific traits (population abundance, distribution or conspicuousness). In large-scale surveys, using a single method that is able to detect most species may be easier, more cost-effective and therefore preferable for conservation planners and managers (Wright et al. 2014). Thus, quantifying the efficacy of sampling methods would help researchers and managers choose the correct survey technique in each case. Specifically, one important aspect of monitoring programs is studying

whether passive survey methods record the same information as active survey methods.

False negatives, i.e. failing to detect a species when it is indeed present, introduce uncertainty in occupancy estimates, decrease the reliability of resulting distribution maps, increase the cost of field surveys and ultimately represent a major component of survey efficiency (Tyre et al. 2003; Wintle et al. 2004). As one of the primary sources of false negatives is the detection method itself, we compare the detectability of 11 mammal species using three passive survey methods (hair snares, camera traps, and scent stations) and two active survey methods (searching for tracks and scats). Hair snares are reported to be useful for cryptic and elusive mammal species (Weaver et al. 2005; Long et al. 2007; Paull et al. 2012). Detection by cameras has been implemented for the last two decades with successful results (O'Connell et al. 2011). Cameras detect a wide range of mammal species but, as with other electronic devices, they are relatively expensive, can be damaged in field conditions, and are more prone to be stolen than less valuable devices. Scent stations (Linhart and Knowlton 1975; Sargeant et al. 1998) allow species identification even on non-appropriate substrates with relatively low cost. Finally, sign surveys are a widespread method for assessing mammal occurrence (Engeman et al. 2000; Dempsey et al. 2014; Soto and Palomares 2015) despite the fact that their efficiency varies with weather conditions and surveyor experience.

Our aim is to evaluate the potential use of hair snares, scent stations, camera traps, and track and scat surveys as mammal monitoring tools in programs. We ask whether different survey methods have similar effectiveness in the ability to detect Iberian mammals and may be considered as alternative tools. On the other hand, if survey methods differ widely in detecting mammal species, some will produce false negatives, which, in turn, may compromise the reliability of monitoring. Specifically, we compare the performance of different survey methods to evaluate whether one of them is able to detect all species occurring in a large area.

1.3 Identification of critical connectivity routes for mesocarnivores across a Mediterranean agroecosystem

The dispersal and persistence of species in fragmented landscapes have been framed within the island biogeography and the metapopulation theories (Hanski and Gilpin 2010; Losos et al. 2010). According to the island biogeography theory, terrestrial habitat patches represent islands within a hostile matrix. According to metapopulation theory, long-term persistence of a species with a patchy distribution depends on the balance between extinction and colonization rates (Hanski 1994). If the extinction rate is higher than the colonisation rate, the species may become locally extinct, which may promote the relaxation and homogenisation of ecological communities (Haddad et al. 2015; Chisté et al. 2018). Hence, species dispersal is critical to preserve biodiversity, as long as it maintains a genetic and demographic flux between populations. Both theories consider a binary space, able or unable to be occupied by species or communities, an assumption that has proved oversimplistic at the landscape scale in terrestrial ecosystems.

Habitat loss and patch isolation play a critical role for species persistence in fragmented landscapes by determining colonization rates (Moilanen and Hanski 1998; Losos et al. 2010) and rescue effects (Brown and Kodric-Brown 1977).

Landscape configuration can favour or impede genetic and demographic flow (Frantz et al. 2010; Uezu and Metzger 2011; Mönkkönen et al. 2014; Herrera et al. 2017). As landscape transformation greatly increases the effects of habitat isolation (Collinge 2009; Magrach et al. 2012; Wegmann et al. 2014), connectivity is usually promoted to counteract biodiversity loss related with habitat depletion (Santos et al. 2016; Martinez Pardo et al. 2017; Xun et al. 2017). Different landscape features represent different levels of resistance to movement for different species (Ricketts 2001), and to some extent species are able to move between habitat patches over certain kinds of landscapes unsuitable for reproduction (Merckx and van Dyck 2007; Powney et al. 2011).

Landscape connectivity can be broadly defined as the degree to which landscape composition and structure facilitates or impedes the movement among habitat patches (Taylor et al. 1993). However, two types of connectivity are distinguished, namely structural connectivity and functional connectivity. Structural connectivity only describes physical relationships between habitat patches, based only on landscape structure (Keitt et al. 1997). Functional connectivity also considers how organisms respond to the quality of landscape elements (Taylor et al. 2006). Considering ecological and behavioural knowledge of functional connectivity measures provides more meaningful predictions of species distribution in fragmented landscapes (Mühlner et al. 2010; Prevedello and Vieira 2010).

Least-cost models are the most extended approach for quantifying functional connectivity (Correa Ayram et al. 2016). These models weight the distance between a source and a target point, based upon species-specific resistance values of the intervening matrix (Adriaensen et al. 2003; Chardon et al. 2003). Some major limitations of the least-cost models are the uncertainty about how organisms actually use the landscape and the existence of biases related to the researcher-perceived landscape structure (Sawyer et al. 2011).

Carnivores are considered suitable models for studying the effects of habitat fragmentation, yet landscape connectivity for carnivores has received little attention. In this study, we first identify the most likely dispersal routes for carnivores between two forest landscapes across a Mediterranean agricultural landscape. As connectivity ultimately represents the behavioural response of animals to hard ecological boundaries (Kindlmann and Burel 2008; Zeller et al. 2012), the motivation underlying the movement of organisms must be taken into account when measuring functional connectivity (Bélisle 2005). We explicitly consider the potential response of model carnivore species to landscape configuration in different scenarios which combine three different factors that are expected to affect species movement across the agroecosystem: size of forest patches, the functional distance between them, and the structural homogeneity of the agroecosystem.

We explore whether the size of forest patches is an important factor determining functional connectivity. We consider that the resistance of the agroecosystem is alleviated by the presence of forest patches and that this function depends upon patch size. Thus, larger areas are more likely to provide enough ecological requirements than smaller areas for transitory establishment, enhancing the chance of successful crossing of the agricultural landscape (Uezu et al. 2005). Then we hypothesise that sets of forest patches close to each other can act as stepping stones (Baum et al. 2004), that is, carnivores can be induced to move along the trajectory connecting nearby forest patches if they can detect one patch from the other, and select such woody cover over open land available in other directions (Stoner et al. 2013). This behaviour could reduce the actual friction of unsuitable habitat between nearby patches. We consider that such increase in permeability depends upon the perceptual ability of carnivores which, in turn, is a function of the separation of nearby patches. Thus, we quantify the resistance to movement of the different landscape elements and hypothesise that resistance values are not constant, but vary with distance to favourable habitats (Taylor et al. 1993; Ferreras 2001). We also hypothesise that that species movement is guided or favoured not by the whole patches but by fine-scale variation in habitat suitability for dispersal around each cell. Therefore, the type of habitat around each pixel is expected to favour or impede connectivity regardless of the actual habitat present in the cell.

We employ dispersal routes as a tool for the identification of sites whose conservation should be prioritised for maintaining connectivity within the agroecosystem. Finally, based on the use made by carnivores of linear elements inside agricultural landscapes (Pereira and Rodríguez 2010; Dondina et al. 2016), we explore how much restoration effort might be needed to enhance connectivity for our model species.

1.4 The influence of landscape heterogeneity on carnivore occupancy of forest fragments in a Mediterranean agroecosystem

The increase in human population and consumption are causing unprecedented demands on natural resources, raising global habitat loss and fragmentation (Foley et al. 2005; Hansen et al. 2013). As a result of the clearing of natural vegetation to favour other land uses, many natural landscapes have been transformed into a mosaic of agricultural fields and other habitats. In these agroecosystems, remnant fragments of natural vegetation constitute a small proportion of the landscape and are surrounded by anthropogenic habitats. As compared with natural habitats, the biodiversity of agroecosystems is greatly reduced (Haddad et al. 2015). Therefore, conservation efforts focused on maintaining biodiversity throughout transformed landscapes has been proposed (Balmford et al. 2005; Rösch et al. 2015).

In fragmented landscapes, species distribution has been extensively described by the patch-matrix model (Mortelliti et al. 2012; Pérez-García et al. 2014) which assumes habitat homogeneity within and between patches as well as a homogeneous matrix. This model also ignores the details of regional processes such as connectivity (Prugh et al. 2008). The dynamics of colonization-extinction in remnant fragments depends on landscape connectivity (Fischer and Lindenmayer 2007), or the degree to which the landscape affects the movement of organisms among habitat fragments (Taylor et al. 1993; Ricketts 2001; Baum et al. 2004). Therefore, measuring connectivity at different spatial scales and using it as a predictor of organisms occupancy in fragments is an undeveloped area of considerable interest.

The influence of landscape connectivity on fragment occupancy has been described using one of two major approaches. Some studies use basic measures such as habitat cover around the fragments or the distance to the nearest suitable habitat patch. Other authors employ the Hanski's connectivity index (Hanski 1999), which combines distance between patches, patch area and species dispersal kernels. These measures are often based on Euclidean

distances, which do not reflect accurately how landscape affect the movement of organisms between fragments (but see Poniatowski et al. 2016). The use of least-cost models (Adriaensen et al. 2003), which represent minimum cost distance between two points, may better capture species response to the textures of habitat quality in agricultural landscapes.

Occupancy of fragments embedded in an agricultural matrix also depends on its permeability to animal movement (Schtickzelle and Baguette 2003; Prevedello and Vieira 2010; Vickers et al. 2015). In landscapes transformed by intensive agriculture, linear elements such as riparian habitats and hedgerows can be employed by wildlife as corridors between habitat fragments (Virgós 2001; Dondina et al. 2016; Santos et al. 2016). Hence, the relative location of the fragments with regard to these linear elements, which could work as main routes of connectivity within the fragment network, may help to explain species occupancy patterns. Indices of connectivity widely used so far seldom consider the specific contribution of each fragment to the connectivity of the whole fragment network.

Fragment occupancy may vary between sectors of agroecosystems featuring internal heterogeneity in structure. Large heterogeneous landscapes may be divided into more homogeneous landscapes, when different ecological processes may govern the distribution of forest species. Occupancy patterns resulting from these processes may fade away or go unnoticed if the whole agroecosystem is analysed as a homogeneous entity. Baum et al. (2004) experimentally verified that in a functionally continuous landscape the importance of fragments for connectivity is reduced. Likewise, the efficiency of fragments for enhancing landscape connectivity is also reduced in very resistant landscapes, where the importance of fragment quality in determining species occupancy will increase. The relative contribution of local context and regional connectivity is expected to be higher in intermediate conditions, where landscape resistance is not as high as to prevent species movement, or as low to allow unrestricted movement across the landscape. Therefore, the relative contribution of fragment quality, local context, and regional connectivity to

explain occupancy patterns is expected to vary with the internal structure of the agroecosystem. Assuming that a landscape is structurally homogeneous, when it is not, may lead to under- or overestimating the contribution of certain landscape predictors on fragment occupancy.

Andrén (1994) described the existence of thresholds in habitat fragmentation that are not linearly related to the proportion of suitable habitat. Small changes around those thresholds of suitable habitat may result in disproportionate changes in species movement pattern which, in turn, might influence species distribution in the landscape. The threshold hypothesis predicts that the occurrence of species will be more affected by habitat fragmentation when the amount of habitat in the landscape is scarce (With and Crist 1995; Jansson and Angelstam 1999; Swift and Hannon 2010). However, little attention has been paid to the influence of fragmentation thresholds on the relative contribution of landscape variables to explain species occurrence (Boscolo and Metzger 2011).

In a Mediterranean agroecosystem, we compare the relative importance of fragment quality, local context and regional connectivity for fragment occupancy by three forest carnivores (the Eurasian badger *Meles meles*, the common genet *Genetta genetta* and the Egyptian mongoose *Herpestes ichneumon*). We also test the hypothesis that the relative contribution of these variables depends on the internal heterogeneity of the landscape (Fahrig 2007). In a heterogeneous matrix with a low resistance to movement, the forest carnivores may be able to select and occupy fragments with a high local habitat quality. Conversely, in a homogeneous matrix with a high resistance to movement, the carnivores may be restricted to fragments that are suitably connected in the fragment network. Thus, in landscapes with a high proportion of habitat left, we expect fragment quality to explain more variation in species occupancy than local context and regional connectivity. In agroecosystem areas with a low proportion of woody cover, we expect the relative importance of local context and regional connectivity variables to be higher than the contribution of fragment quality.

1.5 Regional and local processes of mesocarnivore community assembly in an agroecosystem surrounded by Mediterranean forest

A major goal of ecology is understanding the relative importance of local and regional processes on metacommunity structure (Winegardner et al. 2012; Moritz et al. 2013). The main processes governing the structure of local communities are species-specific dispersal ability, environmental filters and interspecific interactions. Firstly, processes occurring at the landscape and regional scales influence local community composition (Bogoni et al. 2016) by increasing or decreasing the probability of species arrival (Devictor and Jiguet 2007). Thus, the surrounding landscape can have a strong influence on local communities, promoting species colonisation from surrounding areas (Steffan-Dewenter 2003; Xun et al. 2017) or impeding it when habitat deterioration create dispersal filters (Vieira et al. 2009; Laurance et al. 2012; Miller et al. 2015). Secondly, species composition can also vary among local communities due to local habitat quality (Franken and Hik 2004). The probability of colonisation after arrival may diminish as a consequence of a substantial decrease in habitat quality, acting as a filter for the settlement of sensitive species (Pandit et al. 2009; Glorvigen et al. 2013). This process is especially relevant in intensified agricultural landscapes, where land use changes produce the homogenisation of both habitats and ecological communities (Püttker et al. 2015; Chisté et al. 2018). Lastly, community composition can be determined by interactions affecting species co-occurrence patterns such as segregation, aggregation or priority effects (Azeria et al. 2012; Camarota et al. 2016).

Searching for and analysing spatial structures at multiple scales allow hypothesis testing of the processes underlying the variation in species composition (Dray et al. 2012). Modelling patterns of species composition can be used to infer the organisation of ecological communities in homogeneous regions or heterogeneous gradients, determine the strength of the effect of environmental variables, and ascertain the role of spatial structures as spatially autocorrelated

environmental descriptors, as well as its interaction with species-specific differences in dispersal ability. Efforts have been made to quantify the relative effect of local habitat variables, landscape context and spatial structures on the variation in species composition (Grönroos et al. 2013; Heino 2013b; Audino et al. 2017). However, little is known about the relative role of these factors in landscapes with different degree of anthropic pressure.

Dissimilarity in species composition among sites can be partitioned into two dissimilarity components, namely turnover and nestedness (Baselga 2012). The turnover dissimilarity component is related to species replacement, which implies that the simultaneous gain and loss of species is mainly due to environmental filtering. The nestedness dissimilarity component is related to a spatial pattern of species loss due to processes such as selective colonisation or interspecific variation in tolerance to environmental conditions (Si et al. 2016). The relative importance of both components depends on the relative strength of underlying processes governing metacommunity structure (Tonkin et al. 2016). Therefore, analysing the different dissimilarity components we infer the mechanisms driving the variation in species composition (Baselga 2010; Legendre 2014; Gianuca et al. 2017).

As carnivores are especially sensitive to local extinction due to their large home ranges, low densities and external factors as habitat loss and human persecution (Crooks 2002), they are suitable models to study community response to landscape heterogeneity. Our goal is twofold. We investigate whether processes underlying mesocarnivore assembly patterns are associated with species replacement (turnover dissimilarity component) or with a spatial pattern of ordered species loss (nestedness dissimilarity component). We also identify factors affecting variation in mesocarnivore species composition in a Mediterranean agroecosystem surrounded by two forest landscapes with different structure and degree of anthropic pressure. Specifically, we examine the role of the spatial structures, landscape context, local habitat quality, and species interactions in explaining the variation in species composition.

The relative proportion of woody cover in the agricultural landscape and its connectivity for mesocarnivores are too low. Thus, the colonisation of the agroecosystem from surrounding landscapes may be limited, reducing species richness in local communities. If so, we expect a nested pattern in which local communities within the agroecosystem will be subsets of local communities within the forest landscapes (Patterson and Atmar 1986; Wright et al. 1998). We also expect that, in the agroecosystem, a spatial pattern of ordered species loss (nestedness dissimilarity component) will be more important than species replacement (turnover dissimilarity). Further, we expect that the relative contribution of spatial structures and landscape context for explaining the variation in species composition in the agroecosystem will be higher than the relative contribution of local habitat variables or species interactions. Hence, we posit that both spatial and landscape variables will mostly contribute to explain variation in species composition in the study area. Nevertheless, landscape and local habitat variables can be spatially autocorrelated, which makes difficult to infer the relative roles of dispersal and environmental filtering on community structure (Peres-Neto and Legendre 2010; Heino et al. 2015). In this sense, we posit that if species dispersal plays a critical role in the structure of mesocarnivore communities, species with lower movement ability will be underrepresented in the agricultural landscape, while more vagile species will be overrepresented. Conversely, if the influence of dispersal ability on the structure of mesocarnivore communities is negligible, landscape, habitat variables or biotic interactions will be more important drivers of the assembly of local communities.

Finally, as carnivore co-occurrence in local communities may be also influenced by competition or indirect effects (Fedriani et al. 1999; Palomares and Caro 1999), we analyse the effect of interspecific interactions on the variation in species composition. The influence of biotic interactions may be especially relevant within the agroecosystem, where species segregation or aggregation is expected if priority effects operate (Fukami 2015).

2. Materials and methods

Study area

Our work was carried out in a 2,900-km^2 region of the lower basin of the Guadiamar river, southwestern Spain (37º 23'N, 6º 13'W). The basin comprises three distinct landscapes crossed by the river from north to south. The northern landscape, called Sierra Morena, is a large block of natural and semi-natural Mediterranean vegetation (open oak woods, shrublands) interspersed with pine and eucalyptus plantations in rough terrain (Cabezudo et al. 2003). The southern landscape takes its name from the Doñana nature reserve, as it overlaps a large part of the outer fringe of this protected land. The southern landscape was characterised by a mosaic of large pine and oak forest patches, low-intensity agriculture and, to a lesser extent, intensive crops (Cabezudo et al. 2003). A 40-km wide agricultural landscape separates these two forest landscapes. In this agroecosystem, natural vegetation is restricted to narrow strips of riparian vegetation (Borja et al. 2001) and scattered, often small patches of scrubland and open oak forest (Rodríguez and Pereira 2008). Landscape transformation within the agroecosystem has been recorded since, at least, the 15th century (Herrera-García 1980; Borrero-Fernández 1983). Olive groves, vineyards and cereal crops have been the main cultivations along the last 600 years (Herrera-García 1980; Borrero-Fernández 1983), with a decrease in the crop surface during the last century due to land abandonment.

Hereafter, we describe the specific sampling designs, field methods, data and statistical analyses employed to test the different hypotheses raised in the introduction.

2.1 Detection of Iberian terrestrial mammals employing olfactory, visual and auditory attractants

Sampling design and field methods

We distributed 192 detection plots evenly across the three landscapes (Figure M1). On the UTM projection grid, we defined eight 4-km^2 square sampling units

per landscape. We set eight detection plots in each sampling unit, equally distributed among two different detection methods, i.e. four scent stations and four remote cameras. Adjacent sampling units were 2 km apart and considered spatially independent during our short survey periods (see below). Within sampling units, fixed detection plots were spaced at distances > 300 m (mean ± SD = 537 ± 112 m). Trails travelled by mammals were avoided for placing detection plots, so animals had to detour at least a few meters to reach the plot. Scent stations were operated always in dry weather for two consecutive days. Cameras were operated for ten consecutive days.

Early studies showed that operating scent-stations during one or two operative days allow detection of most carnivores and other furbearers (Morrison et al. 1981; Conner et al. 1983; Linscombe et al. 1983; Nottingham et al. 1989), and further effort may not yield higher detection rates (Roughton and Sweeny 1982). A short duration also decreases the chances of repeating the survey due to adverse weather, removes the need of renewing olfactory lures, and helps to hold the assumption of spatial independence among sampling units because the probability that individuals move from one unit to the next is kept low (Roughton and Sweeny 1982).

A pilot study with Iberian carnivores suggested that cameras had to be operative for longer to record at least one of the target species. A ten-day operation period per sampling unit was close to the maximum span we could afford, given the size of the study area and the need to minimize variation in species abundance and environmental conditions. We replicated the survey four times, at six-month intervals, during spring and autumn of 2000 and 2001. During each session, field surveys lasted for six weeks (two weeks per landscape).

Scent stations were circles of shifted sand or earth 0.9 m in diameter where species were identified from tracks printed on smoothed surfaces (Roughton and Sweeny 1982). We used analogical cameras (Canon Prima BF-9s) activated by pressure plates shallowly buried immediately in front of lures (Figure M2).

Figure M1 Sketch of the study area in the lower Guadiamar basin, SW Spain. Left panel shows the limits of three distinct landscapes (A: Sierra Morena, B: Guadiamar Green Corridor, C: northern Doñana) and the position of sampling units (circles). Panels A-C show the detailed placement of detection plots equipped with scent stations (light dots) or remote cameras (dark dots).

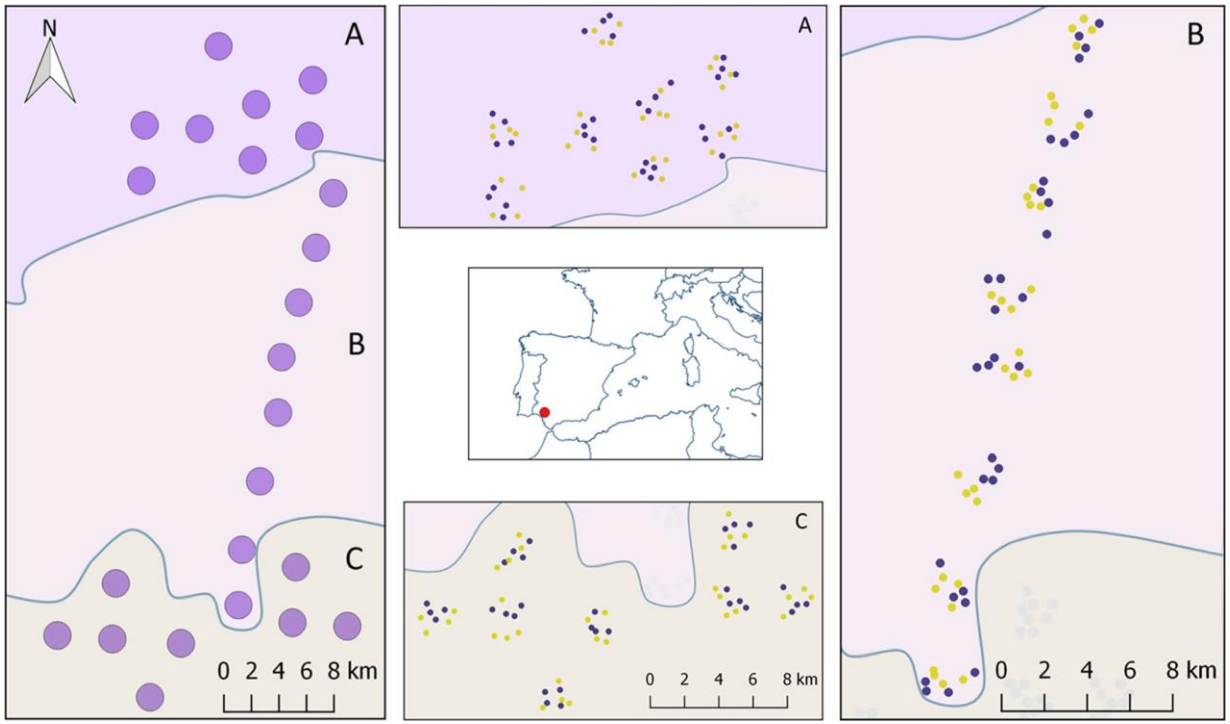

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Figure M2 Top: a compounded lure including olfactory (catnip applied to a calcium sulphate prism), visual (tinsel) and acoustic lures (wooden bells). Bottom: common genet in a detection plot lured with the three types of attractant.

Pressure plates were handcrafted in stiff plastic and had a rectangular shape (33.5 x 25.0 cm). An automatic built-in visible flash operated in the dark. Cameras recorded date and time of mammal visits. A trigger event produced a single picture, and the lapse between successive trigger events was 5 seconds. As cameras could take up to 12 pictures per minute under continuous pressure,

Table M1 The total number of detections and detection frequency for 13 species of Iberian mammals. Detection frequency (DF) is the total number of detections throughout the study divided by the total number of plot-days. To account for low species abundance, detection frequency was corrected by removing the effort (number of plot days) made in sampling units where the species was absent (CDF1) or where the species was absent or scarce (CDF2). Details on the assessment of species absence and scarcity by independent methods are given in Appendix M2.

Species	Common name	Detections	DF (%)	CDF1 (%)	CDF2 (%)
Oryctolagus cuniculus	European rabbit	197	4.28	4.28	8.55
Lepus granatensis	Iberian hare	29	0.63	0.69	3.02
Vulpes vulpes	Red fox	49	1.06	1.06	1.11
Genetta genetta	common genet	42	0.91	1.46	1.56
Herpestes ichneumon	Egyptian mongoose	15	0.33	0.39	0.65
Meles meles	Eurasian badger	8	0.17	0.22	0.60
Martes foina	stone marten	2	0.04	0.21	0.21
Mustela putorius	European polecat	2	0.04	0.52	1.04
Lutra lutra	Eurasian otter	0	0.00	0.00	0.00
Lynx pardinus	Iberian lynx	0	0.00	0.00	0.00
Felis silvestris	wildcat	1	0.02	0.07	0.09
Sus scrofa	wild boar	4	0.09	0.17	0.30
Cervus elaphus	red deer	1	0.02	0.05	0.06

precluded the adoption of a full factorial design and, therefore, acoustic attractants were nested within visual attractants. The visual lure was a piece of silver tinsel 40 cm long stapled by one end to the stake top (Figure M2). This material easily blows in the breeze and shines in the natural light. We used handcrafted wooden wind bells as an auditory lure. Bells were four 20 cm long pieces of cane hanging from a cross-shaped frame and beating a horizontal fixed cane when moved by the wind. Bells were suspended from a rod secured to the stake top. For plots with visual and auditory lures, we used 1.2 m high wooden stakes (Figure M2).

We randomly assigned one scent and the occurrence (or absence) of an additional visual stimulus in a factorial way to the eight plots in each sampling unit. Then we also added the auditory stimulus to two of the plots lured with tinsel, one in a plot scented with FAS, the other in a plot scented with catnip (Appendix M1). Henceforth we refer to the three types of detection plot as olfactory (those lured with scent only; n=96), visual (those lured with scent and tinsel; n=48), and auditory (those lured with scent, tinsel and bells; n=48). On the basis of previous studies (e. g., Martin and Fagre 1988; Chamberlain et al. 1999; Stratman and Apker 2014), we assumed that mammal detection rates using olfactory lures are higher than rates when no lure is used; therefore, we did not employ controls without scents in our design. Further, since we allocated attractants evenly between detection devices, the effect of detection method was controlled for by the sampling design.

For each lure, we recorded the economic cost of materials and quantified the labour needed for preparing and maintaining attractants operative in the field.

Data

For each species and plot, detection was defined as a day in which the species was registered. In each plot, we recorded binary detection/non-detection data on a daily basis, the number of detections, i.e. the number of days a species was recorded in each session (or a different period if specified), and the latency to first detection (LTD; the number of days until first detection within a session).

For each species, we computed detection frequency as the total number of detections throughout the study divided by the total number of plot-days, a measure of sampling effort. Detection rates may be underestimated by computing sampling effort in units where the target species does not occur or is scarce. To avoid this bias, we also computed "corrected detection frequency (CDF)", where we allowed the denominator of this ratio to vary across species by adjusting effort on the basis of independent estimates of occurrence and relative abundance derived from sign surveys (Appendix M2). In CDF1 we did not consider the sampling effort (plot-days) for sampling units where the species was absent; whereas in CDF2 we also removed the effort made in sampling units where the species was scarce (see definitions and procedure in Appendix M2).

We recorded the response of mammals to lures by examining pictures in plots equipped with cameras. We were able to identify three types of behaviour: a) sniffing with head and nose raised to the stake, sometimes leaning forepaws on the stake to reach the lure; b) rubbing neck, flanks or the anal region against the stake or the ground; and c) passing, i.e. animal in movement without apparent interest in the stake. Otherwise, animals were just sitting on the plate, sometimes with their head turned towards the camera, probably distracted or frightened by the flash or the shutter; we considered these cases as undetermined behaviour.

We estimated the percentage of woody cover in a 10-m diameter circle centred at each detection device. Mean daily wind speed was available only for the year 2001 from a weather station within the study area (IFAPA 2016). As a measure of the intensity of natural light in the study area during the night, we obtained the fraction of the moon illuminated each day from (USNO 2016).

We used four variables to characterise the attraction of each mammal species by lures: (a) the binary variable detection; (b) number of detections; (c) probability of detection (POD); and (d) LTD. Variable (b) was computed for the whole study, while variables (c) and (d) were calculated for each plot and session, and variable (a) was the raw presence/absence data recorded for each

plot and day. Further, LTD was computed separately for scent stations and cameras because the period of operation differed between detection methods. Daily records were employed to construct detection histories for each mammal species. To estimate POD for each lure or lure combination, we fitted single-species, multi-season occupancy models to these matrices (MacKenzie et al. 2002) using software PRESENCE v8.3 (Hines 2006).

Analyses

We used contingency tables and the chi-square statistic to test whether the number of detections was the same in plots with FAS and plots with catnip oil, and whether the number of detections was proportional to the availability of plots with olfactory, visual and auditory lures. In addition, we used non-parametric tests to examine whether mean LTD was the same in plots with different scents (Mann-Whitney test), and with different combinations of olfactory, visual and auditory lures (Kruskal-Wallis test).

We used generalised linear mixed models (GLMM) to analyse the effect of lures on detection and LTD, using binomial and Poisson errors, respectively, and specifying the identity of sampling units as a random factor. LTD was only analysed if the type of lure had a significant effect on species detection.

Before examining lure performance, we accounted for factors influencing mammal abundance and activity. As reproduction is seasonal in all species, abundance fluctuates throughout the year, and this may affect detection, especially for rare species. In addition, certain mammal species occur in some landscapes but are absent in others (Rodríguez and Pereira 2008). To control for the potential effect of temporal and spatial variation on species detection in our models, we examined the effect of landscape, session, season, and year. We compared the fit of models containing significant additive effects of these four variables (plus the effect of the detection method in the analysis of LTD) and selected the model with the lowest AIC and the highest Akaike weight (Burnham and Anderson 2002). We considered the selected model as a null model against which we tested lure efficiency. Then we assessed the fit of models also

containing the type of olfactory attractant, in the form of either an additive term or an interaction term with the factors present in the null model. We proceeded in the same way to examine whether the fit of models specifying the type of lure combination was better than that of the null model. GLMM were fit in R (R Development Core Team 2017), using the lme4 package (Bates et al. 2015), and Akaike weights were estimated using the qpcR package (Spiess 2014).

We used occupancy models to analyse the effect of lures on POD. These models simultaneously estimate the probabilities of occupancy and detection (MacKenzie et al. 2002). As we assumed that species presence in each sampling unit did not vary throughout the study, and we were interested in the probability of detection, the probability of occupancy was kept constant in all models. The sequential procedure of model building was similar to that used in GLMMs for detection and LTD. We developed a null model by selecting the most parsimonious occupancy model among those containing factors affecting temporal and spatial variation in detection (landscape, season, session and year). Then we built several sets of occupancy models to examine lure performance against this null model. Firstly, we estimated the probability of detection for each olfactory attractant. Secondly, we compared probabilities of detection for the three levels of lure combination. Finally, only for species where the effects of olfactory lures or lure combination on POD were significant, we specified additional models in order to assess the interaction between environmental covariates and type of lure. As the covariates of interest (cover, wind speed, and nocturnal illumination) were measured at the scale of the detection plot or had one value per day, their influence on lure attraction was only modelled for detection and POD. As wind data were available only for the year 2001, we fitted a complete set of models using only data from 2001 to examine the effect of wind speed on POD.

2.2 Relative efficiency of different survey methods for detecting wild mammals

We focused on large and mid-sized mammals (body mass >800 g) of the orders Lagomorpha, Artiodactyla, and Carnivora, expected to occur in the study area according to an updated mammal atlas (Palomo et al. 2007). Lagomorphs include the European rabbit (*Oryctolagus cuniculus* L.) and the Iberian hare (*Lepus granatensis* Rosenhauer); wild boar (*Sus scrofa* L.) and red deer (*Cervus elaphus* L.) are the only representatives of the order Artiodactyla; and nine species of the order Carnivora occur in the region, namely red fox (*Vulpes vulpes* L.), Egyptian mongoose (*Herpestes ichneumon* L.), Eurasian badger (*Meles meles* L.), Eurasian otter (*Lutra lutra* L.), European polecat (*Mustela putorius* L.), stone marten (*Martes foina* Erxleben), common genet (*Genetta genetta* L.), Iberian lynx (*Lynx pardinus* Temminck) and wildcat (*Felis silvestris* Schreber).

We employed five survey methods that can be classified as active or passive methods, depending on the intervention of surveyors. The passive methods, which do not require the presence of surveyors, were hair traps, scent stations and camera traps. The active methods requiring the direct observation of surveyors were track and scat surveys.

Hair traps consisted of a nylon bristle brush (15 x 7 cm) nailed to a 30 cm high stick. We applied 5 ml of turpentine to the bristles on the first day and another 5 ml five days later. Captured hairs were collected during each visit. The hairs were packed and mounted on slides with nail polish to examine the cuticle structure, and with paraffin oil to observe the structure of the hair core using an optical microscope (x40). Hair samples were identified at the species level whenever possible using keys (Teerink 1991). Scent stations were of 1-meter in diameter consisting of a smooth sand surface whereas analogical cameras were used in camera traps (more details on pages 29-34).

We surveyed mammal tracks and scats along a random path for 90 minutes. The surveyor did not follow a predetermined trajectory but inspected places where finding tracks (trails, unpaved roads, barren or muddy areas) or faeces

(landmarks, trails, crossroads, shores, empty buildings) of the different species was most likely. We recorded the number of faeces and trails of footprints left by each species.

Sampling Design

In each region (see Figure M1), we established eight 4 km^2 square plots separated at least 2 km from each other. We considered the plots as independent spatial replicates. In each of the sampling plots, we placed 10 stations separated by > 300 m from each other (mean ± SD = 537 ± 112 m), equipped with passive detection methods. Hair traps were set in two stations whereas camera traps and scent stations were set in four stations each. Passive detection methods were randomly allocated to the 10 stations. Sign surveys were performed within the limits of sampling plots.

We replicated the surveys four times, henceforth called sessions. Sessions were carried out twice a year, in late spring and late autumns of 2000 and 2001. All sampling plots within a region were surveyed in less than two weeks. In each survey, scent stations were operated for two consecutive days and checked every morning. Hair snares and camera traps were operated for 10 consecutive days. Hair traps were checked on days 5 and 10, whereas cameras were checked on days 1, 2, 6 and 10. Finally, track and scat surveys were conducted only once per temporary replicate.

Data

For each mammal species, we defined three variables: detection/non-detection data, number of sampling units where presence was recorded (i. e., number of detections), and the latency to the first detection (LTD). For hair snares, scent stations and camera traps, records were transformed into a binary variable describing whether each species was detected in each session and sampling plot. Likewise, in natural sign surveys, the number of tracks and scats was

transformed into a binary variable describing whether or not a species was detected in each session and plot.

To assess survey methods for each species, we use six different criteria: number of sampling units where the species was detected, efficiency rate (the relative contribution of each survey method to the total species detection), LTD, unique species detection, the probability of detecting a mammal species by a specific method over the probability of detecting it by other methods, and reliability (ability to produce similar results in temporal replicates).

We ran generalised linear mixed models (GLMM) to model detection depending on the survey method, with sampling plot as the random effect. We employed the "glmer" function in the "lme4" package (Bates et al. 2015) with the binomial family distribution in the R environment (R Development Core Team 2017). To compare the relative efficiency of each method, we employed the odds ratio, which represents the probability of detecting a mammal species over the probability of detecting it by any other method. This represents a measurement of how efficient the survey methods were in comparison to the reference method (the one included in the model intercept).

We also compared method performance in terms of specificity and reliability. Specificity denotes whether certain species were only recorded by specific survey methods, whereas reliability expresses the consistency of a survey method in detecting mammal species throughout the study period. To analyse reliability, we counted the number of times that species were detected in the same sampling plot throughout the sampling sessions when presence was recorded. We then calculated the mean number of times that species were detected across the study area. Hence, detection data were used to assess the effectiveness of the different survey methods employing three different criteria: odds ratio, specificity and reliability.

To analyse the relative contribution of each survey method to the total species detection, we calculated the relative efficiency rate, that is, the number of detections recorded by a single method divided by the total number of detections recorded by any method. We calculated the latency to the first

detection as the time spent during the sampling period until the first species presence was recorded. For passive detection methods, we calculated the mean latency to the first detection during the first two sampling days in every season. For active detection methods, we noted time to the first finding of a track or scat.

2.3 Identification of critical connectivity routes for mesocarnivores across a Mediterranean agroecosystem

Sampling design and field methods

We surveyed four species of Iberian mesocarnivores: the wildcat (*Felis silvestris*), the Egyptian mongoose (*Herpestes ichneumon*), the stone marten (*Martes foina*) and the common genet (*Genetta genetta*). These species have modal dispersal distances varying approximately within one order of magnitude (range 0.6 – 12.1 km) and are associated, in varying degrees, with habitats with a high proportion of woody cover (Stahl et al. 1988; Palomares and Delibes 1991; Genovesi et al. 1997). We used three different survey methods: a) scent stations; b) camera traps; and c) signs surveys (Rodríguez and Delibes 2003; see pages 38-39). For scent stations and camera traps, we distributed 128 detection plots evenly across the two forest landscapes. On the UTM projection grid, we defined 16 4-km^2 square sampling units distributed across the landscapes and we set eight detection plots in each sampling unit, equally distributed among two different detection methods, i.e. four scent stations and four cameras (see pages 29-34). Within each sampling unit, four 90-min random searches for tracks, faeces and other mammal signs at six-month intervals were also conducted (more details on pages 38-39).

Functional connectivity

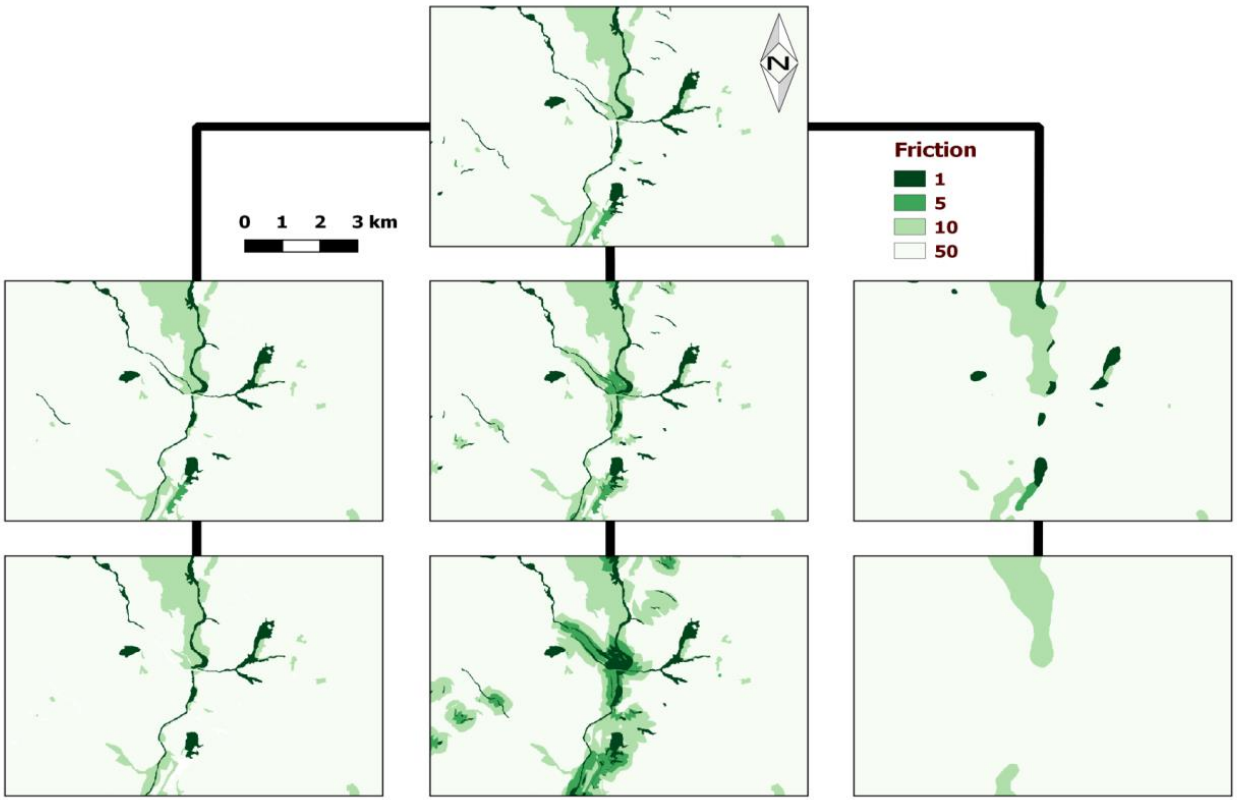
To measure functional connectivity, we developed a least-cost model approach (Adriaensen et al. 2003) by incorporating ecological and behavioural information. To do this, we a) based landscape resistance levels on a consensus among multiple studies analysing species movement in the region; and b) identified dispersal routes in different scenarios, depending on how animals may potentially respond to landscape configuration. We identified 18 habitat types by simplifying a detailed digital map of land uses produced at the time carnivore surveys were carried out (Junta de Andalucía 2016). To do this, we clustered detailed land use types into general categories; for example, urban areas, sport and leisure facilities, roads, rail facilities, construction sites, and similar developments, were clustered into the "Developed areas" category. We assumed that uses clustered in a broader category opposed similar resistance to species movement; otherwise, specific categories were preserved (Appendix M3). Each category, henceforth called habitat type, was assigned a discrete friction value expressing its relative resistance to the movement of the different carnivore species. As resistance surfaces derived from habitat suitability models tend to underestimate landscape connectivity (Ziółkowska et al. 2016), friction was estimated on the basis of reported habitat relationships during dispersal whenever possible; otherwise, habitat preferences of resident individuals were used (Appendix M4).

As there were no explicit natural borders between the forest landscapes and the agroecosystem, we established the limits based on a) an altitude of 140 m in the northern forested landscape, which matched the altitude below which agricultural uses began to be predominant; b) a 1,000 m buffer from forest and shrubland regular patches found in the southern forested landscape; and c) the presence of two large cities, i. e. Huelva (140,985 people) and Sevilla (706,484 people), and their metropolitan areas, as the western and eastern limits, respectively. We calculated least-cost models from the centre of each sampling unit located in the northern forest landscape to the centre of each sampling unit

located in the southern forest landscape. Models were calculated based on the cumulative anisotropic (directional) movement cost (Appendix M5). Resistance values were assigned to cells, and least-cost paths were calculated, on a high-resolution raster with a cell size of 100 m^2.

Least-cost models were estimated in 27 different scenarios, the product of three variables with three levels each (Appendix M6, Figure M3). We created three scenarios, one in which all patches were deemed functional, and two scenarios where patches were considered functional only if they exceeded a certain threshold in size. We identified every forest and scrubland patches within the agroecosystem and divided them into three categories according to their size: less than 3 ha, between 3 and 10 ha, and more than 10 ha. Thus, we created friction maps with all patches, maps only with patches larger than 3 ha, and maps only with patches larger than 10 ha. In these maps, patches smaller than the established threshold were assumed to be unsuitable for species movement.

Figure M3 One representation of friction scenarios for wildcat (*Felis silvestris*) in a raster map with a resolution of 100 m^2. Top panel: original scenario, in which friction values assigned to each cell in the map, only as a function of habitat suitability in the cell (Appendix M3). Left panels: friction in forest patches smaller than 3 ha (top) and 10 ha (bottom) takes the value of unsuitable open agricultural fields. Central panels: friction in cells within 250-m (top) and 500-m (bottom) of forest habitat is reduced one level. Right panels: in each cell friction take the value of modal friction in neighbourhoods of 250-m (top) and 750-m (bottom) in the original map (top panel).


N
0 1 2 3 km
Friction
1
5
10
50

The second variable was the resistance of areas located between forest and scrubland patches. We defined buffers of 250- and 500-m around patches and selected only those intersecting contiguous patches. In these buffers, we reduced the friction value one level in the scale of discrete values. Thus, we obtained a map with original friction values (a scenario assuming no effect of nearby patches), a map where friction was reduced in one level within 250m-buffers and a map where friction was reduced in one level within 500m-buffers. The third variable was the homogeneity of the matrix. We defined the friction value of each $100m^2$-pixel as the result of the modal friction value of 25 (250m) or 75 (750m) pixels around. This way, the presence or absence of small patches of suitable habitat around each pixel favoured or hampered connectivity, regardless of the actual habitat present in the cell.

Critical connectivity sites

Least cost models were used to identify critical connectivity bottlenecks across the agroecosystem. To do this, we combined species-specific least-cost paths for all four carnivore species and defined different sets of paths if they were, at least, 500-m from each other. For each set or bundle of paths, we calculated the total number of least-cost paths. We defined critical connectivity sites as areas with a single bundle of possible trajectories.

Connectivity restoration

We analysed the effects of restoring hedgerows throughout the agroecosystem as a tool for promoting additional connection paths between forest landscapes. To do this, we randomly selected a location inside the agricultural matrix and we digitised a motif that represented approximately 10 ha of hedgerow (Appendix M7). We employed this motif as a model in the subsequent analyses.

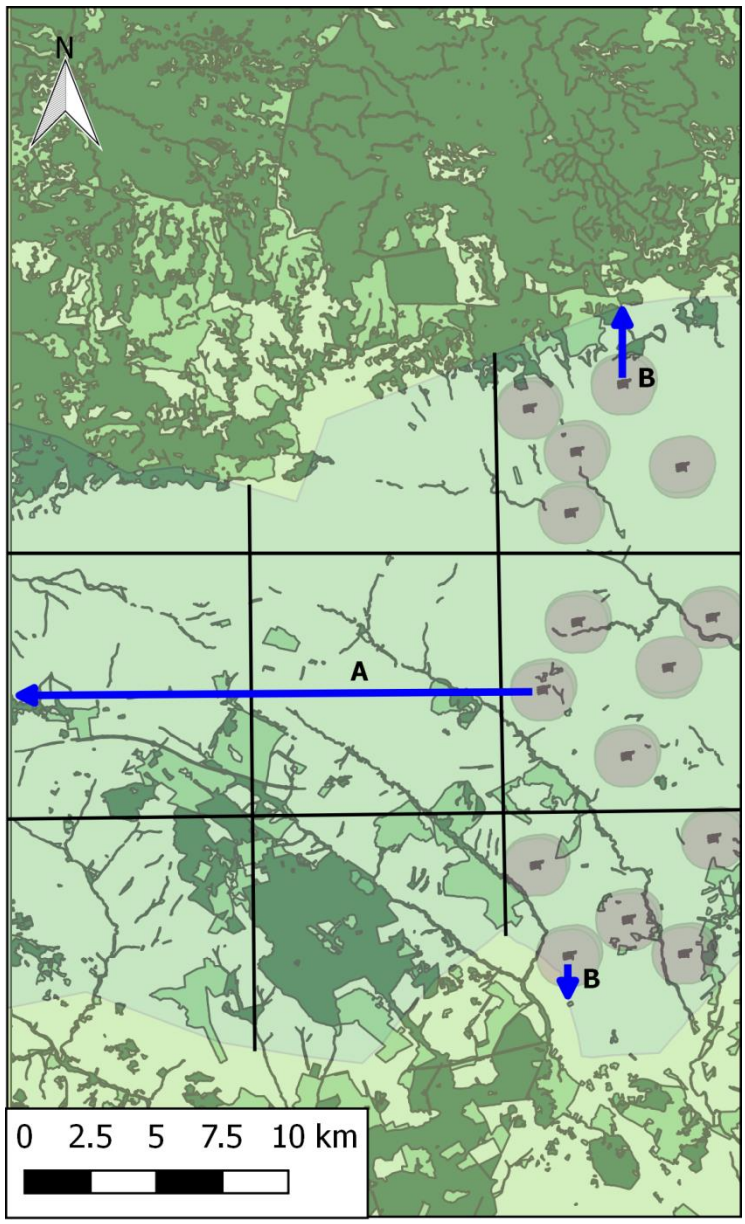
We study the effect of motif location on the creation of new paths for *F. silvestris*. To assess places where the efficiency of the restoration effort would be highest, we created a grid which divided the map extent into nine different

cells, following two gradients: from north to south and from west to east (Figure M4). We divided the agricultural landscape in three bands, where the western band occupied the narrower end of the landscape and the eastern band occupied the wider end (Figure M4). One motif was then randomly placed within the three cells of each band. This was repeated 10 times, changing the location of the motifs inside the cells each time. The same procedure was carried out locating five and ten motifs in each cell. Finally, least- cost paths were calculated between random points in both forest landscapes, in two different scenarios, with and without hedgerows. When the least cost path was different because of the presence of simulated hedgerows, we recorded a new alternative path, and the number of alternative paths was a measure of the effect of hedgerow restoration.

We tested the influence of four different variables on the creation of new potential paths: a) agroecosystem width; b) distance between the restored hedgerows and the forest landscapes; c) local landscape context and d) restoration effort (Figure M4). Agroecosystem width was measured as the distance (m) from the motif to the western limit of the map. The higher the distance to the western limit, the broader the agroecosystem width. Distance to forest landscapes was measured as the minimum distance between the edge of the forest landscapes and the motif (or the closest motif if there is more than one). Local landscape context was measured as the number of suitable habitat patches existing in a 1,000-m buffer around the motifs. Finally, the restoration effort was measured with a factor describing the number of motifs placed in each cell: one, five, or ten. We ran binomial GLM to test the influence of these variables on the creation (1) or not (0) of a new path. We selected the models with the lowest AIC value (Burnham and Anderson 2002).

All analyses were developed using QGIS 2.18 (QGIS Development Team 2017) and R software (R Development Core Team 2017).

Figure M4 One realization of simulations employed to analyse the potential effect of hedgerow restoration on the connectivity of the agroecosystem. The grid delimits nine large cells or regions within the agricultural landscape. The western three-cell band represents the narrow end of the agroecosystem while the eastern three-cell band represents its wide end. Five sets of hedgerow motifs (Appendix M6) were randomly placed in each cell. Shaded circles represent the 1000-m buffer around each hedgerow, where the number of forest habitat patches was calculated. Blue arrows represent A) distance to the western boundary of the study area, and B) distance between the restored hedgerows and the forest landscapes.

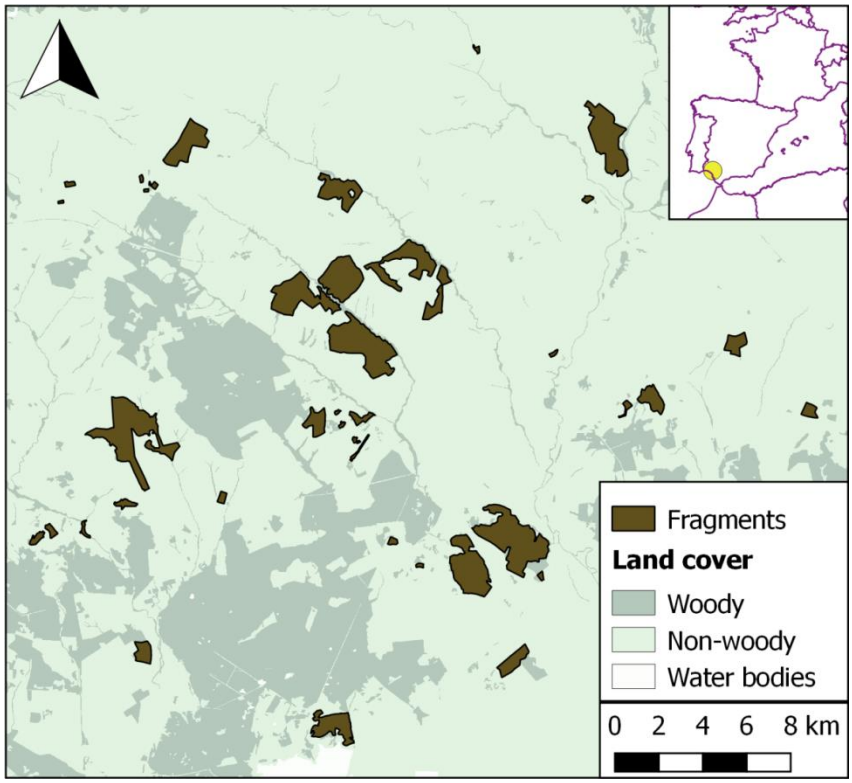

N
B
A
B
0 2.5 5 7.5 10 km

2.4 The influence of landscape heterogeneity on carnivore occupancy of forest fragments in a Mediterranean agroecosystem

Sampling design and survey methods

Based on land use and cover maps (Junta de Andalucía 2016), aerial photos and field work, we identified, checked the position, size, shape, and habitat content of 41 fragments of natural vegetation (2.7-523.6 ha) scattered across the agroecosystem (Figure M5).

Figure M5 The distribution of forest fragments in the agricultural landscape of the Guadiamar River basin, southwestern Spain (37º 23'N, 6º 13'W). Continuous forest habitats, as well as other habitats (grassland anthropogenic, marshland, water bodies), are shown.



We surveyed three carnivores in each fragment using signs surveys (Rodríguez and Pereira 2008). We conducted surveys following dirty roads, paths, animal trails and habitat edges along which carnivores travel and leave their faeces. We set an upper limit for sampling effort in each of three categories of fragment size: <20 ha, up to 60 minutes; 20-50 ha, up to 120 minutes; and >50 ha, up to 180 minutes. For fragments containing more than one habitat type, we stratified sampling by allocating survey effort proportionally to the area of each habitat type. For larger fragments containing only one habitat type, we divided the sampling route into segments of 30 minutes, in order to cover different parts of the fragment. During surveys, we stopped every 10 minutes and in a circle with a radius of 10 m we recorded a) the percent cover of tree canopy, shrubs, grass, and bare ground, b) presence of streams with dense riparian vegetation as a high-quality source of food and shelter, and c) presence of anthropogenic disturbance, including fresh plastic cases of shotgun cartridges (as sign of hunting activity), livestock (sighted or detected by tracks or dung), roads, vehicles, and buildings or other man-made structures inside or in the close vicinity to fragments.

Wild carnivore occurrence was determined on the basis of footprints and faeces, and sampling effort proved sufficient to detect resident species (see details on page 28-29). We did not record signs we could not determine the species level. Surveys were conducted once a year, between April and June of 2001 and 2002. We considered a species was absent from a fragment when no sign was found in any of the surveys.

Landscape variables

Fragment quality. We employed fragment size and the proportion of habitat types as variables representing resource availability within the fragments. Habitat types and streams were identified in land cover maps and checked in the field. For heterogeneous fragments, we also calculated the number of habitat patches and the Shannon diversity index of habitat types. Microhabitat cover and human disturbance scores recorded during surveys were averaged for each

fragment. Means and coefficient of variation were used as descriptors of internal habitat quality.

Landscape context. For each fragment, we recorded the presence of linear elements, such as hedgerows, tree rows or grassy field edges. We calculated the density of shrubby linear elements (m/ha) and the number of woody cover patches in 1-km buffers around fragment boundaries. We also measured the distance to the nearest habitat patch, independently of its size.

Regional connectivity. Since the arrival and eventual colonisation of forest carnivores from the north are less likely, we calculated the distance from each fragment to the boundaries of the Doñana forest landscape (as in page 42). We also measured woody cover in a 5-km buffer around fragment boundaries. We developed two indices of functional connectivity: spatial aggregation of least-cost paths from the Doñana forest landscape for model carnivores (more details on pages 42-43), called Mainstreams; and the contribution of each fragment to regional connectivity, which can be viewed as the performance of the fragment as a stepping stone for carnivores during dispersal (Saura and Rubio 2010).

We employed least-cost paths (Adriaensen et al. 2003) to model connectivity. We assigned species-specific friction values for each dispersal habitat to build cost maps (see page 42), in order to estimate landscape connectivity as it might be perceived by the different species under analysis (Sawyer et al. 2011). These least cost paths were calculated as the cumulative anisotropic (directional) movement cost between specific occupied fragments and points distributed across Doñana forest landscape. We classified fragments depending on whether or not they were located in a buffer of variable size around mainstreams. This binary variable was employed to assess the influence of mainstreams on fragment occupancy (Appendix M8). We expect that fragments close to mainstreams (connected by mainstream buffers) will have a higher probability of carnivore occupancy than fragments located far from mainstreams.

To analyse the specific contribution of each fragment to the connectivity of the fragment network, we combined two different approaches. Firstly, we applied a

metric used in graph analysis, the Betweenness Centrality metric (Freeman 1977), which conceives the landscape as a set of habitat fragments (nodes) and connecting elements (links). The Betweenness Centrality metric indicates how much the focused fragment is involved in the movement of organisms between other fragments, i. e., its role as an intermediate stepping stone in the fragment network. Nodes are characterised by an attribute, and the strength of each link is characterised by the probability of direct dispersal between patches. Regarding the topological position of a fragment in the fragment network, it is possible to analyse the contribution of each fragment to the connectivity between other habitat fragments (Saura and Rubio 2010). Thus, only fragments that become part of the best path for dispersal between two other patches will contribute to the connectivity index. Secondly, we employed the probability of connectivity developed by Saura and Rubio (2010). Saura and Pascual-Hortal (2007) defined the probability of connectivity as the probability that two points randomly placed within the landscape fall into fragments with specific attributes that are reachable from each other given a set of nodes and the links among them. We calculated an index derived from both the Betweenness Centrality index and the probability of connectivity, called BCPC (Bodin and Saura 2010). To assess the importance of each fragment in the network, we calculated BCPC employing area and the proportion of woody cover as fragment attributes (Appendix M9).

Agroecosystem heterogeneity

To analyse the influence of landscape heterogeneity on fragment occupancy, we used an objective method to identify the limit between the mosaic landscape and the simplified landscape. Specifically, we sought the boundary between the two landscapes that maximises the difference in the proportion of woody cover consistently at four spatial resolutions: 10 km^2, 5 km^2, 2.5 km^2, and 1.25 km^2 (Appendix M10).

Statistical analysis

We used Pearson correlation coefficients to test for significant correlations between landscape variables (Appendix M11). When correlations were identified, the variable thought to be of less ecological significance was dropped from the analysis. This procedure was performed separately for the entire agroecosystem, the mosaic landscape and the simplified landscape. As fragment quality variables, we selected fragment area, tree and shrub cover, the presence of a stream with dense riparian vegetation, and occurrence of human disturbance. As predictors for landscape context, we selected the presence of woody linear elements in the matrix between the focal fragment and surrounding patches, or between the focal fragment and the Doñana forest landscape, the density of shrubby linear elements within 1 km-buffer of the fragment, and the distance to nearest habitat patch. Finally, as predictors for regional connectivity, we selected the distance to the Doñana forest landscape and the BCPC index (Table M2).

Model selection

We analysed the effect of fragment quality, landscape context and regional connectivity on the occurrence of carnivores in forest fragments by fitting Generalized Linear Models (GLM) with binomial error and logistic link function. As sample size was small and some variables showed separation problems, i.e., predictors perfectly or quasi-perfectly separates zeroes and ones in the response, we applied Firth's bias reduction of maximum likelihood estimates (Firth 1993; Heinze and Schemper 2002).

Table M2 Selected predictors of fragment occupancy by carnivores. Each group of variables represented different spatial scales: fragment quality (variables measured within the fragments), landscape context (variables measured around fragments), and regional connectivity (variables capturing resistance to movement across the entire agroecosystem).

Fragment quality	
Area	Fragment area (m^2)
Tree	Tree cover (%)
Shrub	Shrub cover (%)
Stream	1 = Presence of stream with dense riparian vegetation in the fragment; 0 = absence
Disturbance	1 = Disturbance within or close to the fragment; 0 = no signs of disturbance
Habitat diversity	Shannon diversity index for habitat uses within the fragment
Landscape context	
Corridor	1 = Presence of woody linear elements between the focal fragment and surrounding patches, or between the focal fragment and DNP
Hedge	Density of shrubby linear elements within 1 km-buffer of the fragment (m/ha)
Dforest	Distance to nearest habitat patch (m)
Regional connectivity	
DDNP	Distance to Doñana forest landscape (m)
BCPC area	Connector fraction of BCPC index with fragment area as fragment attribute
BCPC woody cover	Connector fraction of BCPC index with fragment woody cover proportion as fragment attribute

We performed a backward stepwise regression and, at each step, selected the model with the lowest Akaike Information Criterion (AIC, Burnham and Anderson 2002). Models with ΔAIC < 2 were considered competitive (Sugiura 1978). For each species, we conducted a hierarchical partitioning of the variance explained by each variable retained in the final saturated model (Chevan and Sutherland 1991) with the R^2 goodness-of-fit measure (Cameron and Windmeijer 1997). This involved the calculation of the increase in the fit of all possible models with a particular variable compared to the corresponding increment without that variable (Mac Nally 2002). Hierarchical partitioning allowed the identification of variables strongly affecting the response variable, and to compare them with those having a little independent effect on the response variable (Lemaître et al. 2012).

Spatial analyses were carried out in QGis Software 2.18 (QGIS Development Team 2017). We calculated BCPC index with the software Conefor 2.6 (Saura and Torné 2009). Statistical analyses were done with the R software (R Development Core Team 2017) using the logistf (Heinze and Ploner 2016) and hier.part packages (Walsh and Mac Nally 2013).

2.5 Regional and local processes of mesocarnivore community assembly in an agroecosystem surrounded by Mediterranean forest

Sampling design and carnivore surveys

We assumed that the regional pool of carnivore species can be defined by the occupancy of 10-km cells in updated mammal atlas (Palomo et al. 2007). We surveyed Iberian larger carnivores (body mass > 800 g) using three different methods: scent stations, camera traps and sign surveys (Rodríguez and Delibes 2003; details on page 38-39). In this case, we estimated species composition in each sampling unit by cumulating observations across survey methods throughout the study period.

Spatial variables

Modern techniques such as Principal Coordinates of Neighbour Matrices (PCNM) can generate spatial variables (Borcard and Legendre 2002; Borcard et al. 2004), which represent spatial structures that could be generated by environmental autocorrelation and/or processes such as dispersal (Dray et al. 2006). PCNM analysis consists of three steps. First, we estimated the Euclidean distance matrix between the centres of sampling units. Second, we truncated this matrix for distances longer than 4 km (minimum distance between square centres). Finally, we performed a principal coordinate analysis (which summarises and attempts to represent inter-object distances in a low-dimensional Euclidean space; Gower 1966) to make our spatial information compatible with statistical models. Only principal coordinates associated with positive eigenvalues were kept (see Dray et al. 2006). PCNMs with high eigenvalues (i. e. the first eigenvectors) correspond to broad-scale patterns of spatial association between sampling sites, whereas PCNMs with small eigenvalues (i. e. the last eigenvectors) correspond to fine-scale patterns (Borcard and Legendre 2002). Therefore, a PCNM describes different spatial structures among sampling units across a continuum of spatial scales.

Environmental variables

We assessed microhabitat, macrohabitat and landscape structure for each sampling unit. Variables for each of these three spatial scales are listed and defined in Table M3. We measured microhabitat variables in a 10-m diameter circle centred at each detection device or at regular intervals during sign surveys. Human disturbance was also recorded around sampling points within distances set by the observer's perception. The average value across points (n = 15) was assigned to each 4-km^2 sampling units. Microhabitat variables were considered the local component of environmental variables in the analysis of species composition (see below). Macrohabitat and landscape context variables were extracted from land use and vegetation cover layers (Junta de Andalucía 2016). Macrohabitat variables were measured within each sampling unit,

whereas landscape structure was measured in a 1-km buffer around each sampling unit (i. e., an area of 12 km^2). Macrohabitat variables were considered attributes of the local component of environmental variables, whereas landscape variables were considered the landscape component of environmental variables in the analysis of species composition.

Data analysis

To determine the differences in species composition between the two forest landscapes and the agricultural landscape, species recorded in each sampling unit was considered an independent local community. To quantify dissimilarity in species composition between landscapes, we used the Jaccard's β-diversity index. We calculated multiple-site and pairwise dissimilarity between local communities and computed the turnover and nestedness components of dissimilarity (Baselga et al. 2007; Baselga 2010). Pairwise dissimilarity was calculated using function beta.pair and multiple-site dissimilarity was calculated using function beta.multi, both from "betapart" R-package (Baselga and Orme 2012).

Table M3 Microhabitat, macrohabitat and landscape environmental variables employed in distance-based redundancy analyses. Microhabitat variables were measured around points systematically or randomly spread within sampling units, while macrohabitat and landscape variables were measured on land cover maps of the region. Macrohabitat variables were measured within the boundaries of the sampling units, while landscape variables were measured in a 1-km buffer around the sampling units.

Microhabitat	
Crops/bare	Mean crops and bare ground cover (%)
Grass	Mean grass cover (%)
Scrub	Mean scrub cover (%)
Canopy	Mean canopy cover (%)
CV Crops/bare	Coefficient of variation of crops and bare ground cover (%)
CV Grass	Coefficient of variation of grass cover (%)
CV Scrub	Coefficient of variation of scrub cover (%)
CV Canopy	Coefficient of variation of canopy cover (%)
Disturbance	Degree of disturbance (Low, Medium, High) around sampling points. Signs of human activity, hunting ammunition remnants, traffic noise and presence of human buildings, roads and other infrastructures were recorded

Macrohabitat	
Rabbit	Standardized relative abundance of rabbit (*Oryctolagus cuniculus*) signs
Dog	Standardized relative abundance of dog (*Canis lupus familiaris*) signs
Diversity	Shannon diversity index of land use
Ecotone	Relative proportion (%) of area with adjacent grassland and woody vegetation cover
Riparian	Relative proportion (%) of riparian habitat
Eucalyptus	Relative proportion (%) of *Eucalyptus spp.* forest habitat
Intensive	Relative proportion (%) of intensive crops
Extensive	Relative proportion (%) of extensive crops
Grassland	Relative proportion (%) of grassland cover
Shrubland	Relative proportion (%) of shrubland cover
Canopy	Relative proportion (%) of forest cover excluding

	Eucalyptus plantations
Woody	Relative proportion (%) of shrub and forest cover

Landscape	
DiversityB	Shannon diversity index of land use
EcotoneB	Relative proportion (%) of area with adjacent grassland and woody vegetation cover
RiparianB	Relative proportion (%) of riparian habitat
EucalyptusB	Relative proportion (%) of *Eucalyptus spp.* forest habitat
IntensiveB	Relative proportion (%) of intensive crops
ExtensiveB	Relative proportion (%) of extensive crops
GrasslandB	Relative proportion (%) of grassland cover
ShrubB	Relative proportion (%) of shrubland cover
CanopyB	Relative proportion (%) of forest cover excluding *Eucalyptus* plantations
WoodyB	Relative proportion (%) of shrub and forest cover

To test for nestedness in species composition among local communities, we employed the NODF metric (Almeida-Neto et al. 2008). We evaluated whether nestedness for the observed presence-absence matrix was significantly higher than nestedness expected in 9999 simulated random communities. To avoid incurring type II error, we configured our null models to keep fixed species occurrence but allowed them to randomise the occupancy of sites. In other words, the number of sampling sites in which a given species occurred was kept constant but the identity of sampling sites to which the species was assigned was randomised (Ulrich and Gotelli 2007). We analysed nestedness with the oecosimu function from "vegan" R-package (Oksanen et al. 2017).

To test which combination of spatial and environmental variables best explained the variation in pairwise dissimilarity, we employed distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999; McArdle and Anderson 2001) and variance partitioning (Borcard et al. 1992; Legendre and Legendre 1998; Peres-Neto et al. 2001; Peres-Neto et al. 2006). First, db-RDA was used as a constrained ordination process to summarise the main patterns of variation in dissimilarity matrices that can be explained by both spatial and environmental variables. The total percentage of variation explained by db-RDA was decomposed using the variation partitioning approach, which can be used to infer underlying metacommunity processes when environmental and geospatial data are available (Cottenie 2005). Different fractions of the variation represented independent effects (variation explained by pure spatial or pure environmental variables) and joint effects (variation explained by variables of the two types).

We applied db-RDA and variance partitioning to total dissimilarity and the turnover and nestedness components. First, we scaled the variables dividing the centred values by their standard deviations. Then we selected important explanatory variables using stepwise models for constrained ordination methods following Blanchet et al. (2008). Thus, we selected significant predictors for db-RDAs using two simultaneous stopping criteria: (1) the preselected significance level (α = 0.05), and (2) the adjusted R^2 (i. e., unbiased estimation of the

explained variation, Peres-Neto et al. 2006). As the relationship between the response and individual explanatory variables was also under investigation, a permutation test was used. A total of 9999 permutations were run to randomise dissimilarity and refit the model. Db-RDAs were performed using the capscale function, whereas variance partitioning was carried out employing the varpart function, both from the "vegan" package (Oksanen et al. 2017). Finally, to search for patterns of spatial autocorrelation in environmental variables, we plotted the spatial distribution of the resulting variables and calculated Moran's I (Moran 1950) using Moran.I function from "ape" package (Paradis et al. 2004).

To assess the possibility that differences in species composition between landscapes were caused by species-specific movement ability, we searched the literature for mean natal dispersal distances. As these data were missing for most species we compiled mean distances travelled per day during daily movements, assuming that they were positively correlated with average dispersal distances (Bowman et al. 2002; Bowman 2003). Thus, we considered the mean distance travelled per day as a surrogate or dispersal distance or dispersal ability. We analysed differences between species in the mean distance travelled per day (km/day) employing Cohen's d (Cohen 1988), corrected for small samples:

$$d = \frac{x_i - x_j}{SD} \times \frac{N - 3}{N - 2.25} \times \frac{\sqrt{N - 2}}{N}$$

where x_i represents the distance travelled by species *i*, x_j represents the distance travelled by species *j*, SD is the pooled standard deviation and *N* is the total number of observations employed. We transformed corrected Cohen's d into a correlation coefficient (r) to interpret the magnitude of effect sizes according to Cohen (1988):

$$r = \frac{d}{\sqrt{d^2 + 4}}$$

As a rule of thumb, when r ≤ 0.1, differences in mean distance travelled between species are considered small; when 0.1 ≥ r ≤ 0.243, differences in distance travelled between species are considered medium; and when r ≥ 0.371, differences in distance travelled between species are considered large (Cohen 1988).

To analyse co-occurrence we calculated the C-Score (Stone and Roberts 1990) on a matrix of presence-absence data where rows were mesocarnivore species and columns were sampling units. The C-Score measures pairwise co-occurrence with great statistical power (Gotelli 2000), describing a segregated or aggregated pattern. The larger the C-Score, the less pairwise co-occurrence and more segregated the species are. The number of checkerboard units (CU) for each pair of species was:

$$CU = (r_i - S) \times (r_j - S)$$

where S is the number of sites containing both species, and r_i and r_j are the matrix row totals for species *i* and *j*, respectively. We analysed species occurring at least once in the matrix. Significance was tested using the fixed-fixed null model, in which the row and column sums of the presence-absence matrix are preserved, due to its low frequency of type I and type II errors when tested against random matrices (Gotelli 2000; Gotelli and Ellison 2002). We compared the observed C-Score value from the original matrix with the distribution of values derived from 9999 random matrices. Additionally, a standardised effect size (SES) was calculated as:

$$SES = \frac{observed\ CScore - mean\ simulated\ CScore}{SD\ of\ simulated\ CScores}$$

which indicates the number of standard deviations that the observed C-score is above or below the mean C-score from simulated matrices. High SES of the C-Score describes strong differences between the observed and simulated C-Score values, while low SES represents a small difference. Species co-occurrence

analyses and associated randomisation tests were conducted using the oecosimu function from “vegan” package (Oksanen et al. 2017).

All statistical analyses were performed in R software v3.3.2 (R Development Core Team 2017). Spatial information was obtained and managed using Q-GIS software v2.18.0 (QGIS Development Team 2017).

Appendix M1 Two realisations of the random factorial assignment of lure-detection combinations to eight plots within sampling units.

Scent stations were associated with the FAS/Bells combination in half of the sampling units (i.e. those with an uneven code) and with the catnip/bells combination in the other half (those with an even code). In this example, N denotes sampling units in the northern mosaic landscape, and plot codes are shown in the last two columns.

Lure			Detection method		Sampling unit	
Scent	**Visual**	**Auditory**	**Uneven code**	**Even code**	**N1**	**N2**
FAS			Scent station	Scent station	6	3
FAS			Camera	Camera	5	8
Catnip			Scent station	Scent station	4	5
Catnip			Camera	Camera	3	4

FAS	Tinsel		Camera	Scent station	2	1
FAS	Tinsel	Bells	Scent station	Camera	1	2
Catnip	Tinsel		Scent station	Camera	7	6
Catnip	Tinsel	Bells	Camera	Scent station	8	7

Appendix M2 Corrected detection frequency

Attractant efficiency, as measured by detection frequency, may be underestimated in sampling units where target species are absent or very scarce. In these cases, we computed two variables that accounted for species occurrence, called "Corrected detection frequency 1" (CDF1) and "Corrected detection frequency 2" (CDF2).

Detection frequency was defined as the total number of detections recorded throughout the study divided by the total number of plot-days. For CDF1, the fraction had the same numerator but the denominator was reduced by excluding all plot-days from sampling units where the species was absent. For CDF2, the fraction had the same numerator but the denominator was reduced by excluding all plot-days from sampling units where the species was either absent or scarce.

Species absence and scarcity were assessed during the same sessions of our study period through independent survey methods (i.e. sign surveys with fixed searching effort; Rodríguez and Delibes 2003; authors, unpublished). For species that were not detected by passive detection methods in a given sampling unit, the species was considered absent if it was not recorded during sign surveys either.

To assign scarcity we used the number of signs recorded per sampling units as an estimate of species relative abundance. The maximum number of signs observed was considered as a reference of the potential abundance that a species could reach in the study region. The shape of the ranked-abundance curve typically showed an exponential decrease (Figure M2.1). We conservatively considered that a species was scarce if the number of signs in a sampling unit was <10% of the maximum value observed in the region (Figure M2.1).

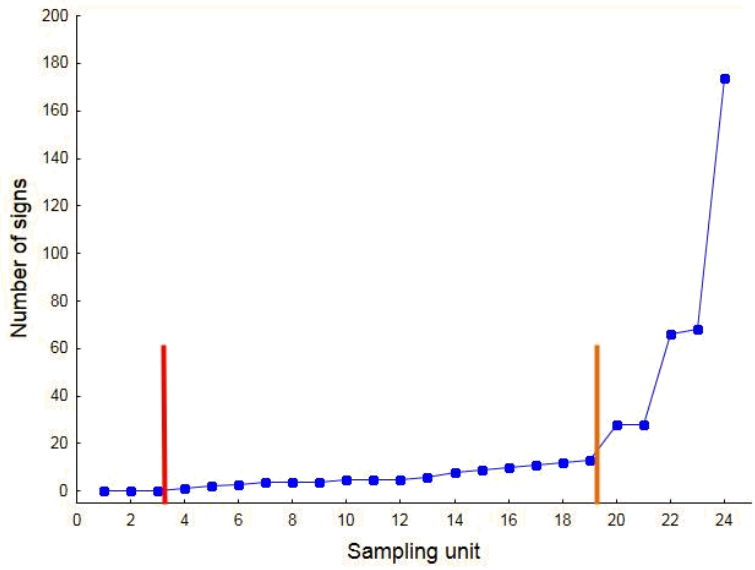


Figure M2.1 Ranked-abundance curve for the Iberian hare in 24 4-km^2 sampling units across the lower basin of the Guadiamar River, SW Spain (author's unpublished data). Sampling units used to compute CDF1 are to the right of the red bar (number of signs > 0). Sampling units used to compute CDF2 are to the right of the orange bar (number of signs > 0.10*max {number of signs}).

Appendix M3 Resistance values assigned to each habitat type and species, based on reported habitat relationships during dispersal whenever possible; otherwise habitat preferences of resident individuals were used (Appendix M4).

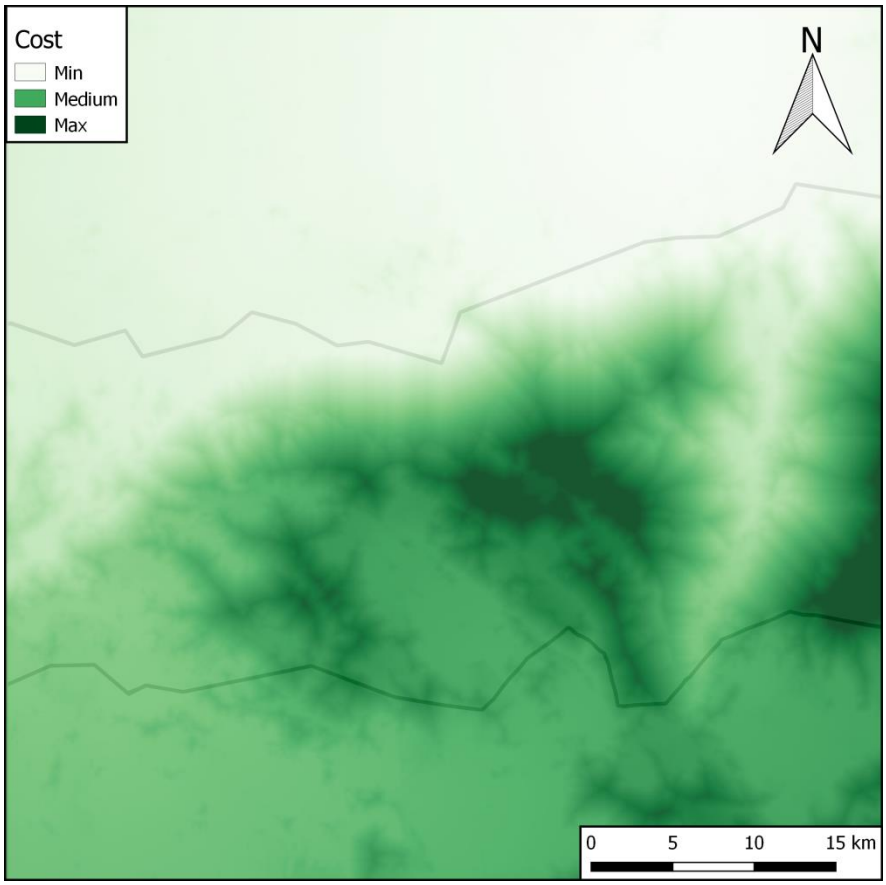
Habitat type	Wildcat	Common genet	Egyptian mongoose	Stone marten
Coniferous forests	1	1	5	1
Mixed forests	1	1	5	1
***Eucalyptus spp* forests**	10	10	10	10
Sclerophyllous forests	1	1	5	1
Riparian vegetation	1	1	1	1
Dense shrubland	1	1	1	1
Dense shrubland + Forest	1	1	1	1
Sparse shrubland + Forest	1	1	1	1
Sparse shrubland + Grassland	1	1	1	5
Natural grassland + Forest	10	1	10	5
Open natural spaces	50	50	50	50
Human infrastructures and urban areas	50	50	50	50
Intensive farming	50	50	50	50
Pastures	10	10	10	10
Agriculture land + natural vegetation	5	5	5	5
Extensive farming	50	50	50	50
Sea and ocean/Intertidal flats	50	50	50	50
Water bodies	50	50	50	50

Appendix M4 Reported habitat relationships during dispersal and habitat preferences of resident individuals for wildcat (*Felis silvestris*), common genet (*Genetta genetta*), Egyptian mongoose (*Herpestes ichneumon*) and stone marten (*Martes foina*). This basis information was employed to the assignation of resistance values to each habitat type.

Species	Model	References
Felis silvestris	High occurrence in mosaics of scrublands and pasturelands.	Lozano et al. 2003
	High occurrence in *Quercus spp* and *Arbutus unedo* forests.	Sarmento et al. 2006
	High occurrence near riparian vegetation, moors, with forests near. Also in Mediterranean shrubland, especially in the mosaic of shrubland, Mediterranean forest and rain-fed crops.	Palomo et al. 2007
	They significantly selected scrublands and avoided crops.	Monterroso et al. 2009
	High occurrence in Mediterranean mountain vegetation.	Lozano 2010
Genetta genetta	The home range included low ash stands (used for resting) and included a great proportion of pine forest and meadows-marsh.	Palomares and Delibes 1994
	High occurrence on 600-1000 masl, in areas where the proportion of shrub cover was high, mean rainfall was low and mean minimum temperature was high.	Virgós et al. 2001
	Forests habitats, associated with the occurrence of rocks and water courses, but it is very generalist. Very abundant in cork and oak woods, Mediterranean shrubland, olive groves, ashes and other riparian vegetation. Also abundant in pine forests.	Palomo et al. 2007
	A high occurrence where the density of trees and shrubs is high, where soil organic matter is present and where there is high vertical vegetation diversity. It is less common in game-state areas. It can inhabit areas with intermediate grazing.	Galantinho and Mira 2009
	High occurrence in *Q. rotundifolia* and *A. unedo* woodlands. Low occurrence in *Erica spp* and *C. ladanifer* scrubland, and in *Eucalyptus spp* stands.	Sarmento et al. 2010
	Resting sites were not included in crops, developed areas, inhabited structures, roads, tracks, paths, but they were included in ravines and torrents.	Camps 2011
	The home range included pine and holm oak forest, ravines, but they did not include crops,	Camps and Alldredge

	lowland sparse maquis vegetation and anthropised areas. Genets moved preferentially within forest patches and close to riparian habitats. Functional connectivity declined with increasing road density but increased with the proximity of culverts, viaducts and bridges.	2013 Carvalho et al. 2016
Herpestes ichneumon	Low occurrence on meadows or marsh, pasturelands and crops. High occurrence in ash stands, *Lentiscus* patches and rushes. Low occurrence in pine forests. Preferable habitats are those with high vegetation cover, with a dense Mediterranean maquis. They are attracted to small water courses and humid zones with dense vegetation. Low occurrence in open areas and areas where lynx occurs. Low occurrence in open areas and high occurrence in areas with dense vegetation, small streams, areas with a groundwater table near the surface and heterogeneous agricultural areas with significant areas of natural vegetation and agro-forestry. Preservation of scrubland patches at low elevation to favour connectivity between populations.	Palomares and Delibes 1993 Palomo et al. 2007 Recio and Virgós 2010 Barros et al. 2016
Martes foina	The home range included high wood proportion. High occurrence with altitude and its correlated variables: high number of forest types, high roughness and low density of human settlements. High occurrence in areas with wood/scrub vegetation and low occurrence in arable lands. In addition, they are attracted to building and watercourses. High occurrence in fragments > 50 ha, and in fragments under 5 km from continuous forest tracts. They occur in a high variety of habitats (moors, Mediterranean forest, sclerophyllous forests and coniferous forests. It tolerates human infrastructures. High occurrence in rural habitats and low occurrence in forest habitats, small patches (< 5 ha) of pastures and orchards, intermediate-sized patches (5-20 ha) of riparian vegetation, median patches (20-50 ha) of both pastures and dense cork oak woodland, and larger patches (50-100 ha) of sparse cork oak woodland.	Genovesi et al. 1997 Virgós and Casanovas 1998 Rondinini and Boitani 2002 Virgós and García 2002 Palomo et al. 2007 Santos and Santos-Reis 2010

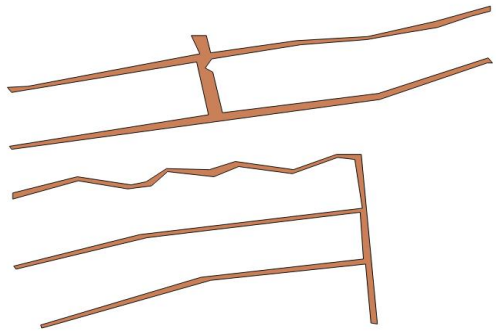
Appendix M5 Relative cost of movement for the wildcat (*Felis silvestris*) between forest landscapes. Light areas represent areas with low friction to movement, whereas dark areas represent high resistance to movement.



Appendix M6 Scenarios representing different friction models depending on the combination of three variables: a) minimum patch size, b) resistance in areas located between natural vegetation patches, and c) fine scale homogeneity around each point of the agricultural landscape. The combination of these three variables resulted in a total of 27 different scenarios.

Scenario	Min. patch area (ha)	Buffer with lower resist. (m)	Adjacent homogeneity (m)
111			0
112		0	250
113			750
121			0
122	0	250	250
123			750
131			0
132		500	250
133			750
211			0
212		0	250
213			750
221			0
222	3	250	250
223			750
231			0
232		500	250
233			750
311			0
312		0	250
313			750
321			0
322	10	250	250
323			750
331			0
332		500	250
333			750

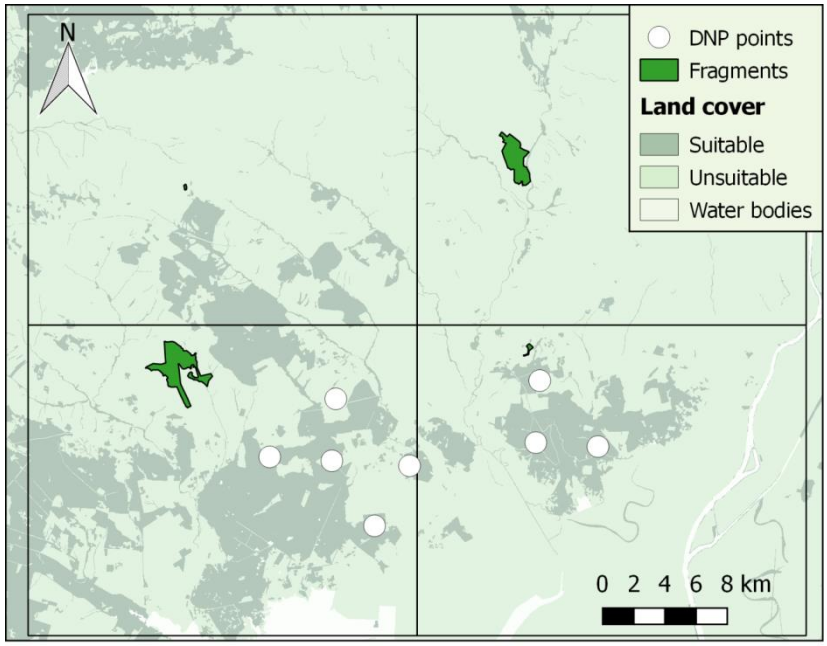
Appendix M7 Motif representing approximately 10 ha of hedgerow surface used as a model for connectivity restoration analyses.



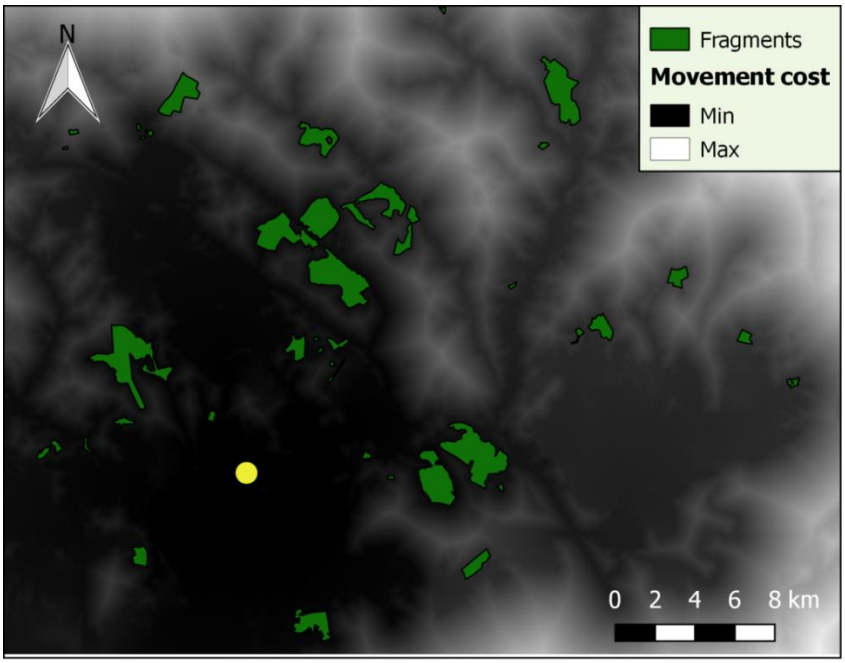
Appendix M8

To analyse the influence of mainstreams on fragment occupancy, we employed least cost paths (LCP; see Adriaensen et al. 2003). First, we estimated movement cost values for each species and land cover type based on the literature (Palomares and Delibes 1991, 1993; Rodríguez et al. 1996; Revilla et al. 2000; Camps Munuera and Llimona Llobet 2004; Rosalino et al. 2004; Santos and Beier 2008; Pereira and Rodríguez 2010). To establish a point of departure and destination, we divided the agroecosystem into four square cells of equal size. To cover as much agroecosystem area as possible, we selected the centroid of fragments delimiting the northern boundary of the species distribution range as destinations. As the sources, we selected eight points distributed across the Doñana forest landscape (see details on page 29, Appendix M8.1). We estimated least-cost paths based on the cumulative anisotropic movement cost (Appendix M8.2). Once we estimated species-specific LCP, we merged them to generate the main movement routes for all the studied carnivores within the agroecosystem, the so-called mainstreams (Appendix M8.3). Finally, we classified fragments depending on whether or not they were located in a buffer around mainstreams. We considered four different buffer widths: 100 m, 250 m, 500 m and 1000 m (Appendix M8.4). This new binary variable was employed to assess the influence of mainstreams on fragment occupancy.

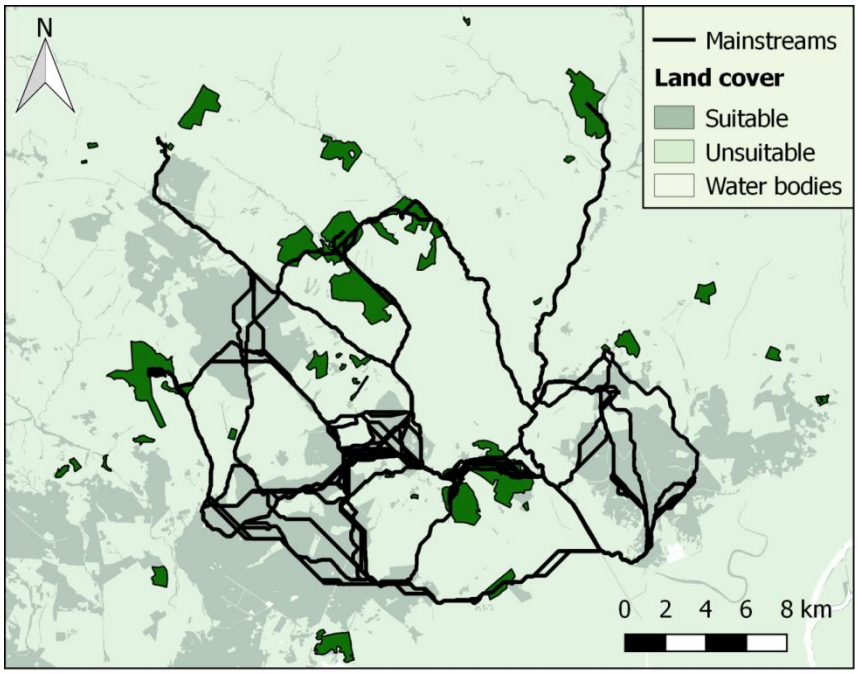
Appendix M8.1 Fragments and points distributed across the Doñana forest landscape, selected as destination and source, respectively, for the least-cost models. To cover as much agroecosystem surface as possible, we selected the centroid of the fragments delimiting the northern boundary of the species distribution range as destinations.



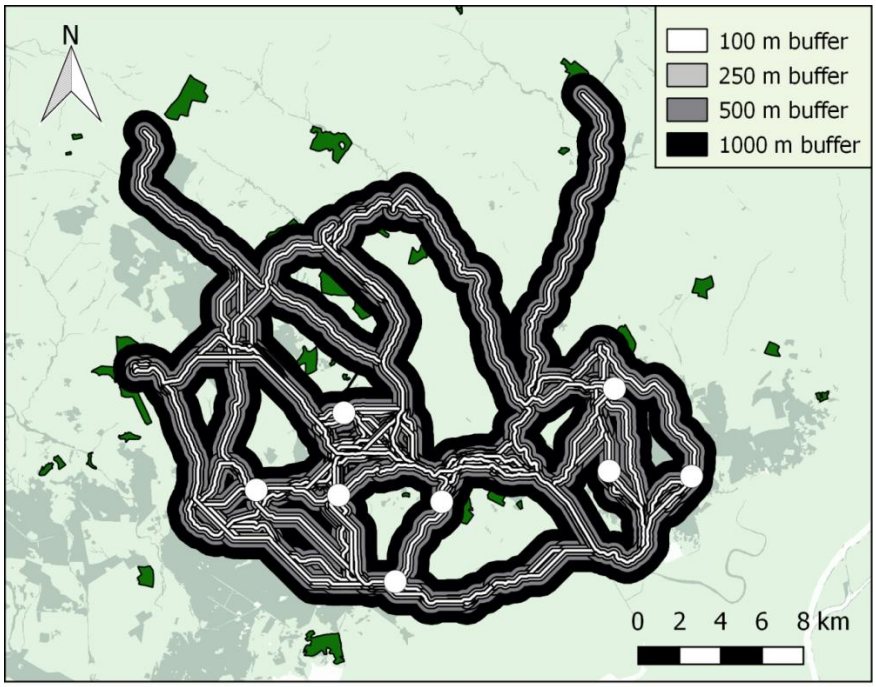
Appendix M8.2 Example of cumulative anisotropic movement cost for least-cost models. Darker areas represent areas with low resistance to movement, whereas lighter areas represent areas with high resistance to movement. The circle represents an example of the beginning of a least-cost path start.



Appendix M8.3 Mainstream paths generated by the combination of the species-specific least-cost models.



Appendix M8.4 Mainstream buffers representing regional connectivity among fragments within the Guadiamar agroecosystem. We classified fragments depending on whether they were or not located in a buffer around mainstreams.



Appendix M9

To measure the contribution of each fragment to regional connectivity, we calculated an index derived from the probability of connectivity (PC) developed by Saura and Pascual-Hortal (2007), and the Betweenness centrality (BC) index (Freeman 1977), called BCPC. Data needed for calculating PC are the number of fragments, the fragment attribute of interest (in our case, fragment area and the proportion of woody cover), and the probability of a species moving directly from one fragment to another, which is computed as a negative exponential dispersal kernel (Saura and Pascual-Hortal 2007). As functional measures of connectivity are more accurate than structural measures (Poniatowski et al. 2016), we quantified the probability of connectivity employing least-cost models (Adriaensen et al. 2003). Finally, we established the probability of connectivity according to the mean maximum dispersal distance recorded for the species under study (Palomares and Delibes 1991, 1994; Rosalino et al. 2005).

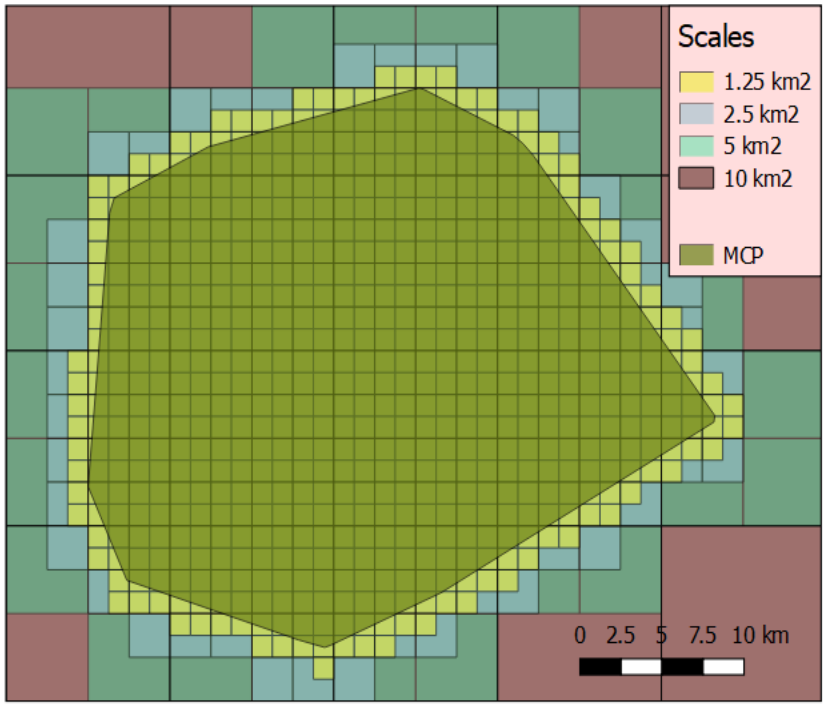
Then we calculated the percentage of variation in the probability of connectivity caused by the removal of each fragment from the landscape (dPC_k). The dPC_k values can be partitioned in different fractions (Saura and Rubio 2010), one of which is the connector fraction ($dPCconnector_k$), which we used to describe the contribution of fragment *k* to the connectivity between other fragments (Saura and Rubio 2010). We also calculated BC to analyse how much fragment *k* is involved in movements between other pairs of fragments by serving as an intermediate stepping stone. Finally, to rank and analyse the contribution of fragments to overall connectivity, we integrated $dPCconnector_k$ and BC (Bodin and Saura 2010). All calculations were developed using Conefor 2.6 (Saura and Torné 2009).

Appendix M10

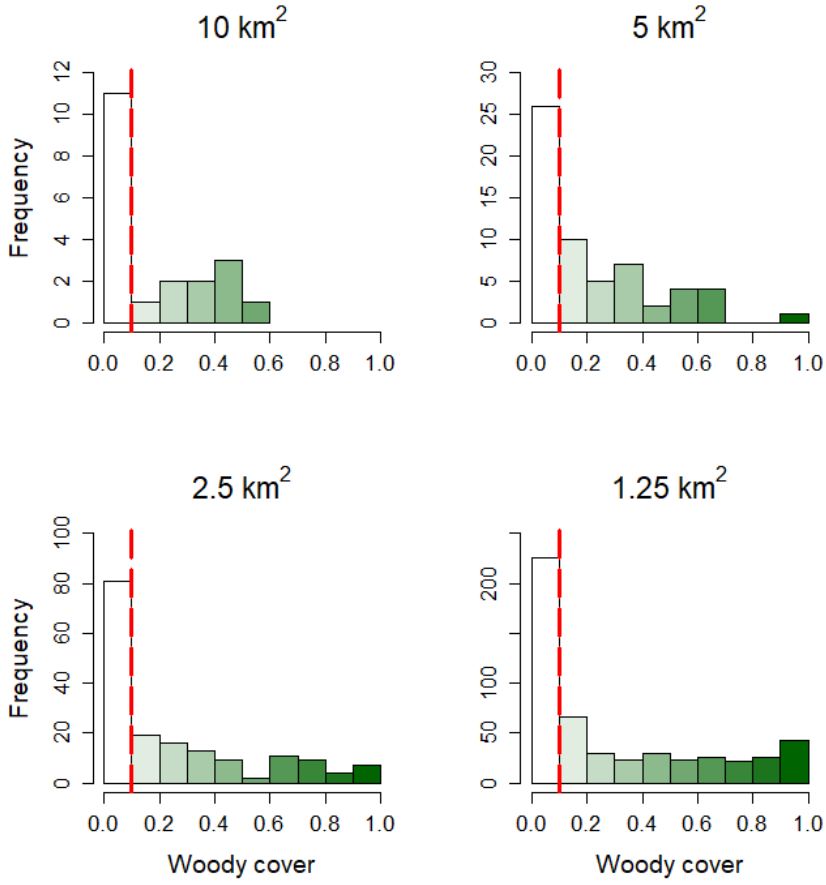
To analyse the influence of heterogeneity within the agroecosystem on the relative contribution of fragment quality, landscape context and regional connectivity to occupancy patterns, we defined the boundary between the mosaic landscape and the simplified landscape. To do this, we first divided the agroecosystem into cells of four different sizes: 10 km^2, 5 km^2, 2.5 km^2 and 1.25 km^2. We calculated the minimum convex polygon encompassing the fragments plus a buffer zone half the size of the cell (Appendix M10.1). Then we calculated the proportion of woody cover (%) in each cell within the minimum convex polygons and analysed the frequency distribution of woody cover for every spatial resolution. We tried different thresholds (0.1, 0.15, 0.2, 0.25 and 0.3) and sought which one consistently discriminated two groups of cells at each spatial resolution. Finally, we calculated the variation in cells with woody cover values higher than the established thresholds for each spatial resolution (Table R13).

Differences were consistently higher when the woody cover was 10% (Appendix M10.2). Therefore, we classified fragments in different landscapes using two criteria 1) a consistency criterion, if fragments were located in cells with high woody cover proportion (> 10%) at every spatial resolution, they were classified into the mosaic landscape. However, if fragments were located in cells with low woody cover proportion (< 10%) in at least one of the spatial resolutions, they were classified into the simplified landscape. Following a continuity criterion, fragments located in cells with a low proportion of woody cover and surrounded by cells with a high proportion of woody cover proportion were classified into the mosaic landscape (Appendix M10.3). Thus, from a total of 41 fragments, 26 were classified into the mosaic landscape, whereas the other 15 fragments were classified into the simplified landscape (Figure R8).

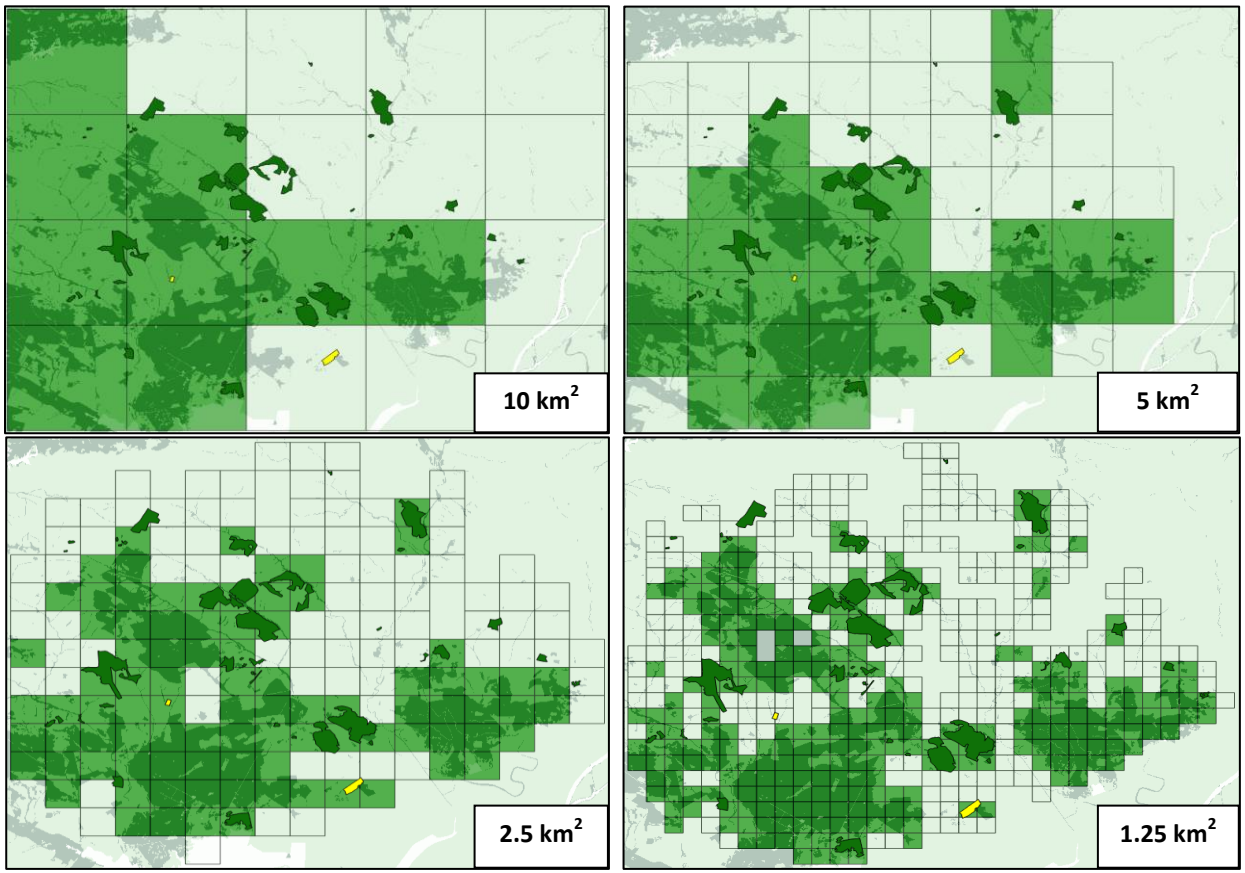
Appendix M10.1 Cell sizes employed to analyse the proportion of woody cover: 10 km^2 (red), 5 km^2 (green), 2.5 km^2 (blue) and 1.25 km^2 (yellow). The minimum convex polygon (MCP) encompassing all forest fragments is also represented (dark green). Buffer distances of half the spatial resolution were applied to this MCP to select the cells in which the relative proportion of woody cover was calculated.



Appendix M10.2 Frequency distribution of the proportion of woody cover (%) for four spatial resolutions: 10 km^2, 5 km^2, 2.5 km^2 and 1.25 km^2. The tail of the distribution began in the range 0.1- 0.4, depending on the spatial resolution. We analysed differences between landscapes in the number of cells of woody cover in the landscape at five different thresholds: 0.1, 0.15, 0.2, 0.25 and 0.3 (see Table R13). Differences were consistently higher for all resolutions when the woody cover threshold was 10% (delimited in the figure by the red line). We employed this threshold value to distinguish between mosaic and simplified landscapes within the agroecosystem.



Appendix M10.3 Distribution of cells with > 10% woody cover (coloured in light green) at each spatial resolution. Agroecosystem heterogeneity was evaluated distinguishing fragments located in high and low woody cover areas. We classified fragments (coloured in dark green) in the different landscapes according to one of two criteria: consistency and continuity. Following a consistency criterion, if fragments were located in cells with high woody cover proportion (> 10%) in all spatial resolutions, they were classified into the mosaic landscape. However, if fragments were located in cells with low woody cover proportion (< 10%) in any of the spatial resolutions, they were classified into the simplified landscape. Following a continuity criterion, fragments located in cells with a low woody cover proportion that were surrounded by cells with high woody cover proportion were classified into the mosaic landscape (coloured in yellow).


10 km²
5 km²
2.5 km²
1.25 km²

Appendix M11 Pearson's correlation coefficient (r) between landscape variables. Variables excluded from the analyses were those correlated with fragment area, which was kept due to its importance determining species occupancy (Prugh et al. 2008; Mortelliti et al. 2012; Pérez-García et al. 2014). Excluded variables included the number of habitat patches within the fragment (Habitat Patches), the number of habitat patches in 1-km buffer around fragments (Habitat patches buffer), the proportion of patches with woody vegetation in 5-km buffers around fragments (Forest availability), the density of patches with woody vegetation in 5-km buffers around fragments (Forest density), and regional connectivity based on least-cost models (Mainstreams). In addition, the distance between fragments (Dfrags) was excluded due to its correlation with the distance to the nearest forest patch (Dforest), a classic measure of connectivity. Significant correlations ($P < 0.05$) are noted with *.

	Area	Tree	Shrub	Habitat Patches	LU diversity	Stream	Disturbance	Linear Elements	Habitat Patches Buffer	Hedge	DDNP
Area	1.00										
Tree	0.18	1.00									
Shrub	-0.04	-0.20	1.00								
Habitat Patches	0.56*	-0.02	-0.03	1.00							
LU diversity	0.28	0.00	-0.13	0.00	1.00						
Stream	0.48*	0.08	0.24	0.37*	0.05	1.00					
Disturbance	-0.25	-0.19	-0.18	-0.13	0.21	-0.46*	1.00				
Linear Elements	0.09	0.22	0.23	0.32*	0.00	0.31*	-0.04	1.00			
Habitat Patches Buffer	0.52*	0.22	0.22	0.16	0.33*	0.43*	-0.08	0.39*	1.00		
Hedge	0.16	-0.02	-0.13	0.44*	0.11	0.18	0.00	0.29	-0.10	1.00	
DDNP	-0.05	-0.05	-0.08	-0.11	-0.15	-0.04	-0.01	-0.04	-0.40*	0.40*	1.00
Dfrags	0.22	0.31*	-0.06	0.01	0.11	0.36*	-0.27	-0.08	0.06	-0.26	0.06
Dforest	-0.05	0.26	-0.16	-0.21	-0.09	0.13	-0.08	-0.23	-0.33*	0.02	0.40*
Forest Availability	-0.24	-0.19	0.12	0.03	0.14	-0.03	0.14	0.29	0.27	-0.02	-0.55*
Forest Density	0.60	0.08	0.13	0.12	0.17	0.20	-0.28	0.09	0.57*	0.02	-0.02
BCPC_area_Mm_conn	0.17	0.28	0.01	0.02	0.00	0.01	0.06	0.02	0.06	-0.06	-0.11
BCPC_cover_Mm_conn	0.20	0.31	0.04	-0.07	0.26	-0.10	0.09	-0.10	0.07	-0.14	-0.13
BCPC_area_Gg_conn	-0.08	0.43	-0.25	-0.11	0.08	-0.29	-0.04	-0.10	0.16	-0.04	-0.22
BCPC_cover_Gg_conn	-0.17	0.41*	-0.25	-0.15	0.03	-0.30	-0.01	-0.08	0.14	-0.07	-0.21
BCPC_area_Hi_conn	0.19	-0.14	-0.21	0.41*	-0.15	0.12	-0.14	0.12	-0.08	0.21	-0.04

BCPC_cover_Hi_conn	-0.09	0.14	-0.24	-0.01	0.04	-0.19	0.02	-0.22	-0.08	0.00	-0.23
Mainstream 1000m	0.34*	0.20	0.00	0.30	-0.02	0.16	0.00	0.35	0.23	0.16	-0.27
Mainstream 500m	0.48*	0.12	0.14	0.43*	-0.01	0.33*	-0.20	0.45*	0.22	0.13	-0.06
Mainstream 250m	0.49*	0.14	0.07	0.38*	-0.06	0.39*	-0.27	0.41*	0.24	0.17	-0.01
Mainstream 100m	0.53*	0.09	0.00	0.40*	0.01	0.34*	-0.23	0.37*	0.21	0.20	0.03

	Dfrags	**Dforest**	**Forest availability**	**Forest density**	**BCPC_area_Mm_conn**	**BCPC_cover_Mm_conn**
Dfrags	1.00					
Dforest	0.58*	1.00				
Forest Availability	-0.23	-0.44*	1.00			
Forest Density	-0.18	-0.35*	-0.28	1.00		
BCPC_area_Mm	0.17	0.13	-0.23	0.10	1.00	
BCPC_cover_Mm_conn	0.21	0.15	-0.22	0.21	0.73*	1.00
BCPC_area_Gg_conn	-0.18	-0.16	0.19	0.03	-0.03	0.09
BCPC_cover_Gg_conn	-0.19	-0.17	0.20	0.01	-0.10	0.02
BCPC_area_Hi_conn	-0.05	-0.10	0.11	0.06	-0.04	-0.09
BCPC_cover_Hi_conn	-0.25	-0.16	0.29	-0.19	-0.10	0.07
Mainstream 1000m	-0.24	-0.26	-0.02	0.15	0.29	0.13
Mainstream 500m	-0.12	-0.25	-0.19	0.31*	0.12	0.00

Mainstream 250m	-0.09	-0.22	-0.19	0.36*	0.15	0.16
Mainstream 100m	-0.16	-0.20	-0.28	0.39*	0.15	0.03

	BCPC_area_Gg_conn	**BCPC_cover_Gg_conn**	**BCPC_area_Hi_conn**	**BCPC_cover_Hi_conn**	**Mainstream 1000m**	**Mainstream 500m**	**Mainstream 250m**	**Mainstream 100m**
BCPC_area_Gg_conn	1.00							
BCPC_cover_Gg_conn	0.97*	1.00						
BCPC_area_Hi_conn	-0.01	-0.03	1.00					
BCPC_cover_Hi_conn	0.59*	0.56*	0.27	1.00				
Mainstream 1000m	-0.10	-0.15	0.14	0.02	1.00			
Mainstream 500m	-0.23	-0.27	0.17	-0.17	0.78*	1.00		
Mainstream 250m	-0.21	-0.26	0.18	-0.15	0.75*	0.95*	1.00	
Mainstream 100m	-0.20	-0.25	0.20	-0.14	0.71*	0.90*	0.95*	1.00

3. Results

In this section, we show the results obtained in each of the studies addressed in this thesis.

3.1 Detection of Iberian terrestrial mammals employing olfactory, visual and auditory attractants

We detected eleven target species, or 85% of potentially occurring species. Among them, six species were recorded <10 times (Table R1) and were not considered in further analyses. After a total effort of 4608 plot-days (768 plot-days with scent stations plus 3840 plot-days with cameras), we recorded 350 detections (Table R1) which yields a detection frequency of 7.6% for all mammal species combined. A total of 194 (55.4%) and 156 detections (44.6%) were recorded in FAS-scented plots and catnip-scented plots, respectively, and these overall frequencies were significantly different from the expectation of equal detection rates ($\chi^2 = 4.126$, $P = 0.042$). Differences between olfactory attractants were not significantly different for any mammal species (Table R1).

Only 14% of pictures showed mammals passing, apparently without paying attention to the lure (Table R2). For lagomorphs, this proportion (21%) was larger than for carnivores (7%). Behaviour was undetermined in 72% of lagomorph pictures, whereas 73% of carnivore photographs showed an active and positive response to the lure (sniffing or rubbing; Table R2). Small sample size precluded a formal comparison of the three types of attractant at the species level. Overall frequencies of active responses (sniffing and rubbing) were similar between the two types of scent (Table R2).

Considering lure combination, the number of detections in plots with olfactory, visual, and auditory lures was 186 (53.1%), 98 (28.0%), and 67 (19.1%), respectively. These frequencies were also significantly different from the expected ratio 2:1:1 ($\chi^2 = 6.732$, $P = 0.034$) because the proportion of detections at plots with acoustic lures was significantly lower than the predicted value (0.25). The number of red fox (*Vulpes vulpes*) detections in plots set with scent only was higher than expected, whereas the number detections in plots with

visual or acoustic attractants were significantly less than expected (Table R1). The common genet (*Genetta genetta*) visited plots with visual lures more than expected, but this difference was not significant after adjusting for multiple comparisons (Table R1).

Models of detection yielded disparate results across species. We found a significant positive effect of visual lures as compared with other lure combinations in the common genet, significant negative effects of visual and auditory lures for the red fox, and a significant negative effect of auditory lures for the European rabbit (*Oryctolagus cuniculus*; Appendix R1). The Iberian hare (*Lepus granatensis*) and the Egyptian mongoose (*Herpestes ichneumon*) were detected in proportion to the availability of scents and lure combinations (Table R1, Appendix R1). A single model of detection including the interaction between lure combination and environmental covariates affecting visibility fitted the data well, but the effect of this interaction was not significant (see the second model for the red fox in Appendix R1).

Overall, mean latency to the first detection did not vary between scents. A similar attraction by FAS and catnip was found in separate analyses for each species (Table R1). Mean LTD varied little among types of compounded lures (Table R1). Likewise, models for the red fox and the common genet did not show any significant effect of lure type on LTD (Table R3).

The small number of detections precluded the estimation of POD in plots operated with cameras, so POD was estimated from scent station data only. The probability of mammal detection did not vary significantly with the type of scent used (Mann-Whitney $U = 65$, $P = 0.713$) or the combination of lures present in plots (Kruskal-Wallis $H = 0.350$, $P = 0.839$). For the Iberian hare and the Egyptian mongoose, the most parsimonious POD model was the null model (Table R4). The top-rank model for the European rabbit described a negative effect of woody cover on POD only in plots with the visual lure combination (Wald $\chi^2 = 4.931$, $P = 0.026$). For the common genet, the most parsimonious model did not contain the effect of lure type on POD whereas, for the red fox, the best model described a positive but non-significant relation (Wald $\chi^2 = 2.237$, $P = 0.135$)

between POD and olfactory lures (Table R4). Contrary to our expectation, covariates affecting visibility did not improve the fit of occupancy models containing lure type only (Table R4). The interaction between visual lures and cover entered some competitive models of POD (Table R4), but this effect was not significant.

Concerning the hypothesis on the role of temperature on scent volatility, the effect of the season only entered null models for two out of five species (Table R4, Appendix R1). Further, in species for which the effect of season on detection (Appendix R1), LTD (Table R3), or POD was significant (Table R4), the response during the colder season (autumn) was always higher than in the warmer season (spring).

Olfactory lures were quite inexpensive in terms of money and effort needed to set and maintain scents operative throughout the survey session (Table R5). Visual lures were slightly more expensive but equally easy to set and keep. Instead, the wooden bells we used as an acoustic lure were about eight times more expensive than the other lures because bells were handcrafted and the cost and time of labour were considered (Table R5). However, the effect of scent lasts only for a few days whereas bells and, to a lesser extent, tinsel strips did not need to be replaced during the whole study, which could reduce their cost-effectiveness ratio.

Table R1 Number of detections and mean time (days) to first detection (LTD) of mammal species exposed to two scents (FAS and catnip oil) and different combinations of lure types.

	Scent type				Lure combination[a]				
Species	FAS	Catnip	Statistic[b]	P	Olfactory	Visual	Auditory	Statistic[b]	P
Number of detections									
Oryctolagus cuniculus	112	85	3.701	0.054	104	55	38	3.548	0.170
Lepus granatensis	17	12	0.862	0.353	13	11	5	2.793	0.247
Vulpes vulpes	26	23	0.184	0.668	36	7	6	10.84	0.004[c]
Genetta genetta	21	21	0.000	1.000	15	18	10	6.907	0.032
Herpestes ichneumon	9	6	0.600	0.439	7	5	3	0.600	0.741
Mean LTD									
Scent stations									
Oryctolagus cuniculus	1.34	1.44	994.0	0.331	1.31	1.44	1.53	2.830	0.243
Lepus granatensis	1.18	1.00	22.5	0.374	1.20	1.00	1.000	1.286	0.526
Vulpes vulpes	1.45	1.39	169.0	0.720	1.31	1.80	1.57	4.835	0.089
Genetta genetta	1.63	1.50	21.0	0.707	1.80	1.50	1.40	1.625	0.444
Herpestes ichneumon	1.33	1.40	8.0	1.000	1.33	1.50	1.33	0.156	0.925

Cameras									
Oryctolagus cuniculus	3.10	3.25	43.5	0.779	3.67	1.67	4.67	3.395	0.183
Lepus granatensis	2.50	5.20	9.0	0.156		5.20	2.50	2.635	0.105
Vulpes vulpes	4.33	4.00	2.5	1.000	3.25	8.00		2.105	0.147
Genetta genetta	3.33	4.43	23.0	0.827	3.33	5.00	3.00	3.791	0.150
Herpestes ichneumon	5.75	2.00	1.0	0.717	6.00	1.00		2.105	0.147

[a] Olfactory: scent only; Visual: scent plus tinsel; Auditory: scent plus tinsel plus bells.

[b] Goodness of fit tests are shown. Statistic refers to χ^2 for the analysis of the number of detections and for the approximation to Kruskal-Wallis *H* in the analysis of mean LTD across lure combinations and to Mann-Whitney *U* for the analysis of mean LTD between scents.

[c] Significant difference once the Bonferroni correction for multiple tests was applied (α/m, where α = 0.05 and m = 5 species).

Table R2 Frequencies of behaviour recorded in pictures for three mammal taxa in detection plots lured with different scents. Undetermined means that animal behaviour could not be clearly assigned to any of the other three classes.

	Sniffing		Rubbing		Passing		Undetermined	
	FAS	Catnip	FAS	Catnip	FAS	Catnip	FAS	Catnip
Lagomorphs	2	12	0	0	8	4	23	19
Carnivores	15	12	3	3	2	1	4	5
Ungulates	0	1	0	0	0	0	0	0
Total	17	25	3	3	10	5	27	24

Table R3 Comparison of generalised linear mixed models of latency to the first detection. Only models for mammal species whose detection was significantly affected by the type of lure are shown. The null model for the red fox contains Season and Method of detection as factors, whereas the null model for the common genet includes Year and Method of detection. Other models considered also include the main effect of lure type (factor Type), and its interaction with factor retained in the null model. Only models with good fit, defined by $\Delta AIC \leq 2$, are shown. AIC: Akaike Information Criterion. w_i: Akaike weights.

Species	Model	AIC	ΔAIC	w_i
Vulpes vulpes	Season + Method	125.70		0.600
	Season + Method + Type	126.87	1.17	0.334
Genetta genetta	Year + Method	105.09		0.731

Table R4 Fit indicators for models of probability of detection (POD) for five species of Iberian mammals. The null model contains a single factor, either Landscape, Season or Year, depending on the species. Other models considered also include the main effect of lure type, its interaction with Landscape, Season or Year, and the interaction between levels of Type and covariates potentially affecting visibility. Only models with good fit, defined by ΔAIC ≤ 2, are shown. AIC: Akaike Information Criterion. w_i: Akaike weights

Species	Model	AIC	ΔAIC	w_i
Oryctolagus cuniculus	Landscape + Season + Visual*Cover	673.54		0.300
	Landscape + Season + Olfactory	673.89	0.35	0.252
	Landscape + Season + Cover + Visual*Cover	675.50	1.96	0.113
Lepus granatensis	Landscape	163.51		0.304
	Landscape + Visual	165.16	1.65	0.133
	Landscape + Olfactory	165.39	1.88	0.119
	Landscape + Auditory	165.43	1.92	0.116
	Landscape + Visual*Cover	165.48	1.97	0.113
Vulpes vulpes	Landscape + Olfactory	300.98		0.404
	Landscape + Auditory	301.82	0.84	0.266
Genetta genetta	Season + Cover	144.69		0.268
	Season + Visual*Cover	145.40	0.71	0.188
	Season	146.20	1.51	0.126
Herpestes ichneumon	Year	86.87		0.443
	Year + Auditory	88.28	1.41	0.219
	Year + Visual	88.87	2.00	0.163

Table R5 The estimated cost of using each type of lure.

Calculations are shown for one survey session and per detection plot. Cost is expressed in terms of time and money. As scents lasted only a few days, the economic cost of scents for the whole study was fourfold the reported figure. In contrast, all bells and most tinsel strips could be reutilised in the four sessions, thus reducing its overall cost.

	Survey session			Detection plot		
	Money (€)	Labour (€)	Time (h)	Money (€)	Labour (€)	Time (min)
Lure						
FAS	123	24	3.2	1.3	0.2	2
Catnip	162	36	4.8	1.7	0.4	3
Tinsel	206	12	1.6	2.2	0.1	1
Wooden bells	787	398	53.6	16.4	8.3	67
Travel	765			4.0		

3.2 Relative efficiency of different survey methods for detecting wild mammals

All mammal species known to be present were recorded in the study area during the sampling period (Table R6). However, some species, such as the Iberian lynx or the polecat, were detected only in a few sampling plots (see Table R6). Detections recorded using hair snares were excluded from the analyses because only domestic species (horse and dog) were found. No species were exclusively recorded by a single survey method. However, we found that five species were only recorded by active methods, namely red deer, wild boar, Eurasian otter, stone marten and Iberian lynx (Table R6).

We found significant differences in the number of detections between survey methods (Kruskal-Wallis $\chi^2 = 12.648$, df = 3, $p = 0.005$), with the main differences found between track surveys and camera traps ($\chi^2 = 4.64$, $p = 0.006$) and track surveys and scent stations ($\chi^2 = 3.38$, $p = 0.079$). Only track surveys detected all target species across the study area (Table R6). On average, using track surveys, we recorded species more frequently than with other methods, whereas with camera traps we detected mammal species less frequently than with alternative methods (Figure R1). Differences across methods in the number of detections for stone marten were remarkable, as this species was not detected by any passive method and most of the signs found were faeces (Table R6).

We also found significant differences in the relative contribution of different methods to overall detection (Kruskal-Wallis $\chi^2 = 13.724$, df = 3, $p = 0.003$). Major differences were found between track surveys and camera traps ($\chi^2 = 4.77$, $p = 0.004$) and track surveys and scent stations ($\chi^2 = 3.54$, $p = 0.060$). Track surveys showed the highest relative contribution to the total number of detections (Figure R2). Furthermore, the contribution of track surveys to the total number of detections in seven species was 100%, and they also contributed > 70% to the total number of detections in 11 species (Table R7). The

contribution of camera traps was very low. The contribution of scat surveys to the detection of the Eurasian otter and the stone marten was notable.

Due to differences in the duration of the operative period, differences in LTD were analysed separately for passive and active methods. On average, scat surveys showed the lowest LTD among active detection methods whereas scent stations showed the lowest LTD among passive detection methods (Table R8). However, no significant differences were found between scent stations and camera traps ($t = 0.964$, $df = 6.987$, $p = 0.367$; Figure R3A), or between track and scat surveys (Mann-Whitney $U = 59$, $p = 0.314$; Figure R3B).

Although track surveys showed the highest reliability (Table R9), we did not find significant differences among methods (Kruskal-Wallis $\chi^2 = 3.380$, $df = 3$, $p = 0.337$; Figure R4). Therefore, provided that species were detected, survey methods showed a similar consistency in detecting mammal species repeatedly throughout the study period.

The effect of survey method on species-specific detection is shown in Appendix R2. Differences in odds ratio between survey methods were significant (Table R10). For most species, the odds ratio of track surveys was significantly higher than the ratio of other survey methods. For the Eurasian otter and the stone marten, track surveys were less efficient than scat surveys, whereas, for the Iberian lynx, differences in odds ratio were not significant (Table R10).

Table R6 Number of sampling plots where each species was recorded by the different survey methods during the study period.

	Survey method				
	Passive detection		Active detection		
	Scent stations	Camera traps	Track surveys	Scat surveys	All
Lagomorpha					
O. cuniculus	23	11	24	23	24
L. granatensis	8	4	16	18	22
Artiodactyla					
S. scrofa	0	0	12	5	12
C. elaphus	0	0	10	7	10
Carnivora					
V. vulpes	16	5	24	23	24
H. ichneumon	5	4	17	3	20
M. meles	6	1	19	4	19
L. lutra	0	0	11	15	15
M. putorius	1	1	1	1	3
M. foina	0	0	1	5	5
G. genetta	11	10	17	6	20
L. pardinus	0	0	1	1	1
F. silvestris	1	0	6	0	6

Figure R1 Mean number (± SE) of sampling plots where mammal species were detected by four different survey methods. For each method sample size was the number of species detected in the whole study area using that specific method.

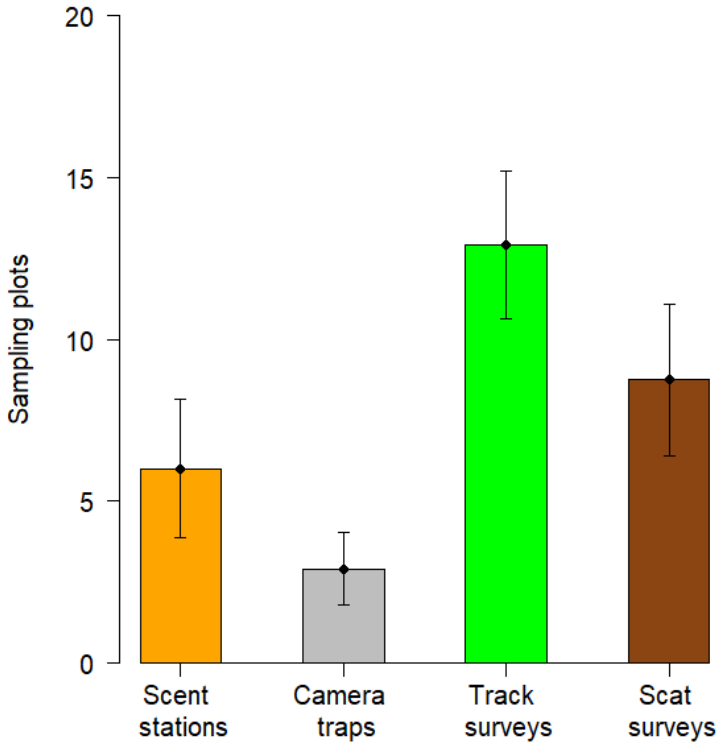


Figure R2 Mean Relative Efficiency Rate (± SE), measured as the number of detections recorded by a given method divided by the total number of detections recorded by any method. For each method sample size was the number of species detected in the whole study area using that specific method.

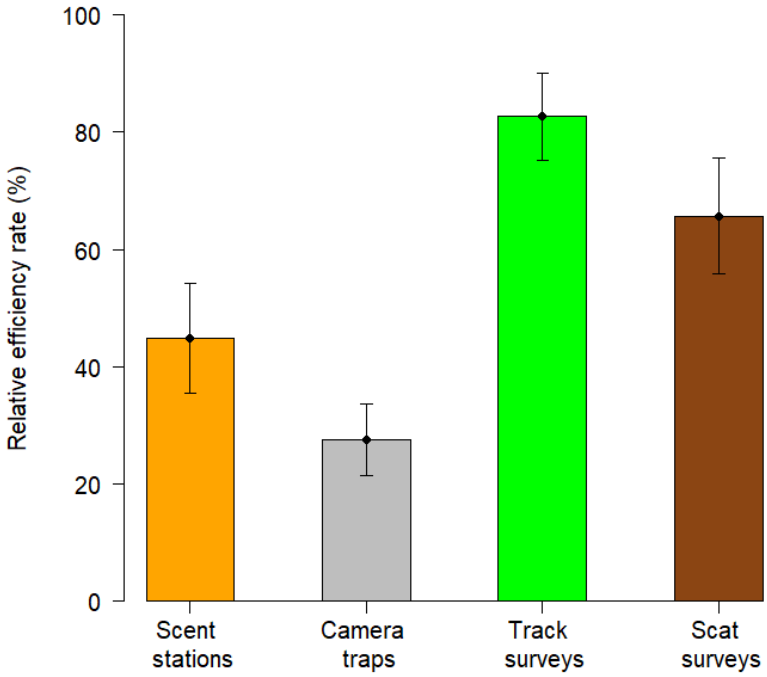


Table R7 Relative efficiency rate or the relative contribution (%) of each sampling method to the total number of detections for each species (Table R6).

	Survey method			
	Passive detection		**Active detection**	
	Scent stations	**Camera traps**	**Track surveys**	**Scat surveys**
Lagomorpha				
O. cuniculus	96	46	100	96
L. granatensis	36	18	73	82
Artiodactyla				
S. scrofa	0	0	100	42
C. elaphus	0	0	100	70
Carnivora				
V. vulpes	67	21	100	96
H. ichneumon	25	20	85	16
M. meles	32	5	100	21
L. lutra	0	0	73	100
M. putorius	33	33	33	33
M. foina	0	0	20	100
G. genetta	55	50	90	32
L. pardinus	0	0	100	100
F. silvestris	14	0	100	0

Table R8 Average latency to first detection for each mammal species.

	Survey method			
	Passive detection		Active detection	
	Scent stations	Camera traps	Track surveys	Scat surveys
Lagomorpha				
O. cuniculus	31.88	44.40	0.18	0.17
L. granatensis	29.00	48.00	0.39	0.37
Artiodactyla				
S. scrofa			0.44	0.23
C. elaphus			0.30	0.25
Carnivora				
V. vulpes	31.83	24.00	0.23	0.24
H. ichneumon	32.00	36.00	0.51	0.09
M. meles	39.00		0.60	0.21
L. lutra			0.53	0.63
M. putorius	24.00		0.02	0.02
M. foina			1.30	0.63
G. genetta	34.67	40.00	0.50	0.36
L. pardinus			0.33	0.67
F. silvestris	48.00		0.54	

Figure R3 Mean LTD (± SE) of each survey method, that is, the time to the first record of each species. A) Mean LTD differences between passive methods; B) mean LTD differences between active methods. For each method sample size was the number of species detected in the study area using that specific method.

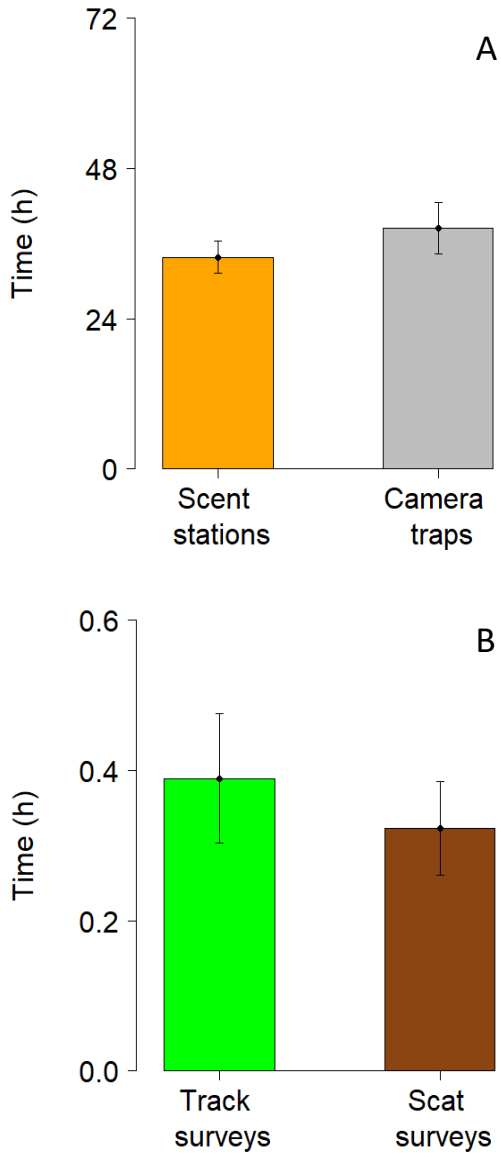


Table R9 Mean reliability, or the number of sessions in which the occurrence of mammal species was recorded.

	Survey method			
	Passive detection		Active detection	
	Scent stations	Camera traps	Track surveys	Scat surveys
Lagomorpha				
O. cuniculus	2.43	2.18	3.46	3.61
L. granatensis	2.00	1.50	2.06	2.06
Artiodactyla				
S. scrofa			1.67	1.40
C. elaphus			2.80	1.71
Carnivora				
V. vulpes	1.94	1.00	3.33	2.87
H. ichneumon	1.25	1.20	2.65	1.00
M. meles	1.17	1.00	1.95	1.00
L. lutra			1.73	2.53
M. putorius	1.00	1.00	1.00	1.00
M. foina			1.00	1.60
G. genetta	1.50	1.09	1.88	1.33
L. pardinus			1.00	1.00
F. silvestris	1.00		1.17	

Figure R4 Mean reliability (± SE), or mean number of sessions that species were detected in the same sampling plot throughout the study period, provided that species presence was recorded.

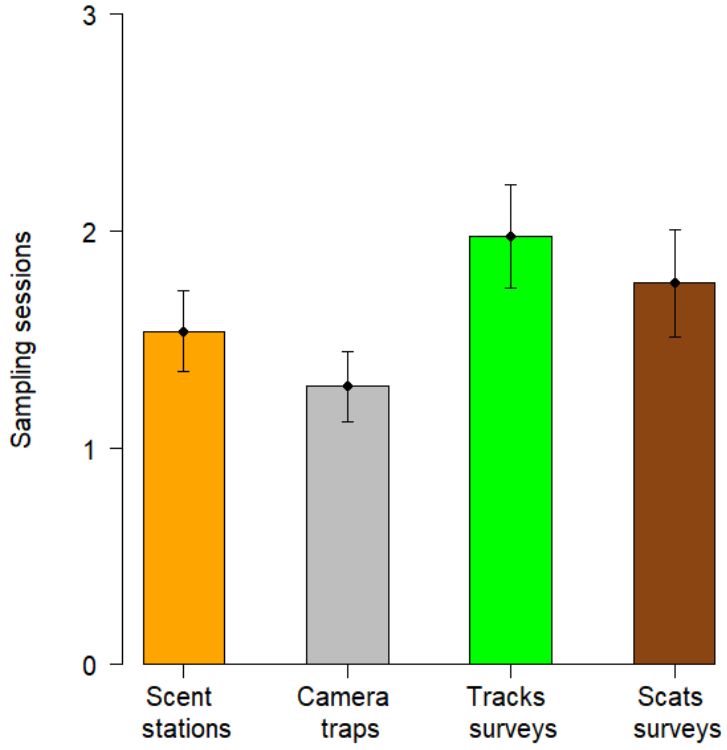


Table R10 Odds ratio, as an index of the relative efficiency of survey methods for species detection. Odds ratio describes how efficient a method is compared to the reference method (odds ratio = 1). The higher the value, the more efficient the survey method, and *vice versa*. Models for the common genet did not converge and are not shown. * $p < 0.05$

	Survey method			
	Passive detection		**Active detection**	
	Scent stations	**Camera traps**	**Track surveys**	**Scat surveys**
Lagomorpha				
O. cuniculus	9.24*	1.00	52.47*	52.47*
L. granatensis	4.53*	1.00	23.41*	18.12*
Artiodactyla				
S. scrofa			4.73*	1.00
C. elaphus			9.25*	1.00
Carnivora				
V. vulpes	9.7*	1.00	125.80*	52.05*
H. ichneumon	1.23	1.00	27.67*	0.57
M. meles	6.46	1.00	69.46*	4.17
L. lutra			0.23*	1.00
M. putorius	1.00	1.00	2.29	2.29
M. foina			0.07*	1.00
L. pardinus			10.00	1.00
F. silvestris	1.00		8.64*	

3.3 Identification of critical connectivity routes for mesocarnivores across a Mediterranean agroecosystem

A total of 5,900 least-cost paths were calculated between the forest landscapes for all four carnivore species. The different simulated scenarios regarding specific potential responses to landscape configuration provided different functional distances between forest landscapes (Table R11; Appendix M6). Major differences in functional distance were found when connectivity was reduced due to the exclusion of small habitat patches as suitable dispersal habitats, and when we considered the fine scale homogeneity around each pixel (Table R11). Differences in functional connectivity were also detected between species, especially in the case of the Egyptian mongoose, the common genet and the wildcat (Table R11). Functional distances calculated for Egyptian mongoose increased only when large habitat patches were considered as suitable habitat for dispersal (scenarios 2xx and 3xx; Table R11). Functional distances for the Egyptian mongoose were, in general, lower than functional distances for other species (Table R11). In the case of the common genet, functional connectivity decreased notably due to high fine scale homogeneity around each point of the agricultural landscape (scenarios xx2 and xx3; Table R11). Finally, functional connectivity for the wildcat was enhanced when resistance level between habitat patches was reduced (scenarios x2x and x3x; Table R11).

In general, our results show more alternative routes in the forest landscapes, where agricultural fields are uncommon than within the agroecosystem (Figure R5). However, least-cost models also reflect movement patterns inside forest landscapes. In the northern forest landscape, we identified an area of approximately 6,640 ha which was avoided under every simulated scenario. This area was mainly characterised by the presence of *Eucalyptus spp.* plantations, open areas and a few scattered shrubland patches. In the southern forest landscape, we identified a site with a high concentration of paths (2,331 paths, 39.5%). This area contained olive groves and coniferous plantations.

Least-cost paths crossing the agroecosystem were clustered across three different regions (Figure R5). Two of these regions were characterised by a high concentration of paths, one was located in the western limit of the agroecosystem (3,043 paths, 51.6%), whereas the other one was located in the eastern limit of the agroecosystem (2,857 paths, 48.4%). We also identified a region in the centre of the agricultural landscape which contained a very low proportion of paths (17 paths, < 0.1 %).

Critical connectivity sites

Within the agroecosystem, least-cost path concentrated in four different critical connectivity sites (Figure R6). Three of these sites were distributed in the two major bundles of routes: one was located in the west, where the agroecosystem gets narrow (3,043 paths, 51.6%), and the other one was located along the riparian habitat of the Guadiamar River in the east (2,857 paths, 48.4%). In the western sector of the agricultural landscape, critical connectivity sites differed substantially in the number of paths per bundle: whereas one was composed of 2,996 routes (50.8%), the other one was composed of 47 routes (0.8%). Along the eastern bundle, critical connectivity sites concentrated 2,857 paths (48.4%).

Connectivity restoration

New routes were created in 18.9% of the total number of simulated hedgerow restorations. The most parsimonious model of connectivity restoration was the saturated additive model, that is, the one containing all predictors (Table R12). Nevertheless, only agroecosystem width had a significant negative effect (Table R12). Most of the new alternative routes (65.4%) appeared when the distance to the western limit of the agricultural landscape was < 1,842 m (Figure R7).

Table R11 Functional distances (km) resulting from least-cost models under different scenarios. Scenarios were identified with a code of three numbers representing the degree of modification from the original map (1 = no changes in the variable; 2 = moderate changes in the variable; and 3 = large changes in the variable). For example, scenario 213 represent a map in which "2" represents that friction values of small (< 3ha) habitat patches takes the value of unsuitable open agricultural fields; "1" represents that original friction values are kept in cells between habitat patches, and "3" represents that in each cell friction takes the value of modal friction in neighbourhoods of 750-m in the original map.

Scenario	Wildcat	Stone marten	Common genet	Egyptian mongoose
111	65.1	65.2	64.2	65.5
112	86.2	86.0	48.6	88.1
113	115.0	115.5	114.8	44.3
121	60.6	61.2	59.8	60.7
122	90.1	81.1	84.0	NA
123	NA	108.0	111.7	57.5
131	58.4	54.1	58.4	79.0
132	79.2	75.0	49.2	110.4
133	46.0	104.7	112.3	61.2
211	59.1	63.3	61.1	85.1
212	84.6	84.7	79.1	111.4
213	114.3	111.2	41.9	60.5
221	60.4	58.4	60.5	81.1
222	82.7	80.2	48.8	105.7
223	106.2	107.6	112.9	57.1
231	58.5	57.3	54.5	62.7
232	77.9	109.2	49.3	106.7
233	110.0	108.4	113.4	59.7
311	63.0	63.2	79.0	90.6
312	85.8	87.2	87.3	111.5
313	112.5	109.7	NA	59.6
321	58.3	58.0	57.1	85.5
322	65.3	109.2	48.0	108.6
323	109.9	111.9	115.5	55.4
331	58.1	55.8	55.5	47.8
332	83.2	65.7	48.6	107.0
333	110.8	109.6	48.6	112.5

Figure R5 Least cost paths between 64 pairs of sites, eight in each of the forest landscapes (dark colours) north and south of the Guadiamar agricultural landscapes (light colours). Lines represent a total of 5,900 pathways for common genet, Egyptian mongoose, wildcat and stone marten, using species-specific friction values representing the resistance of each habitat type to the movement of carnivores.

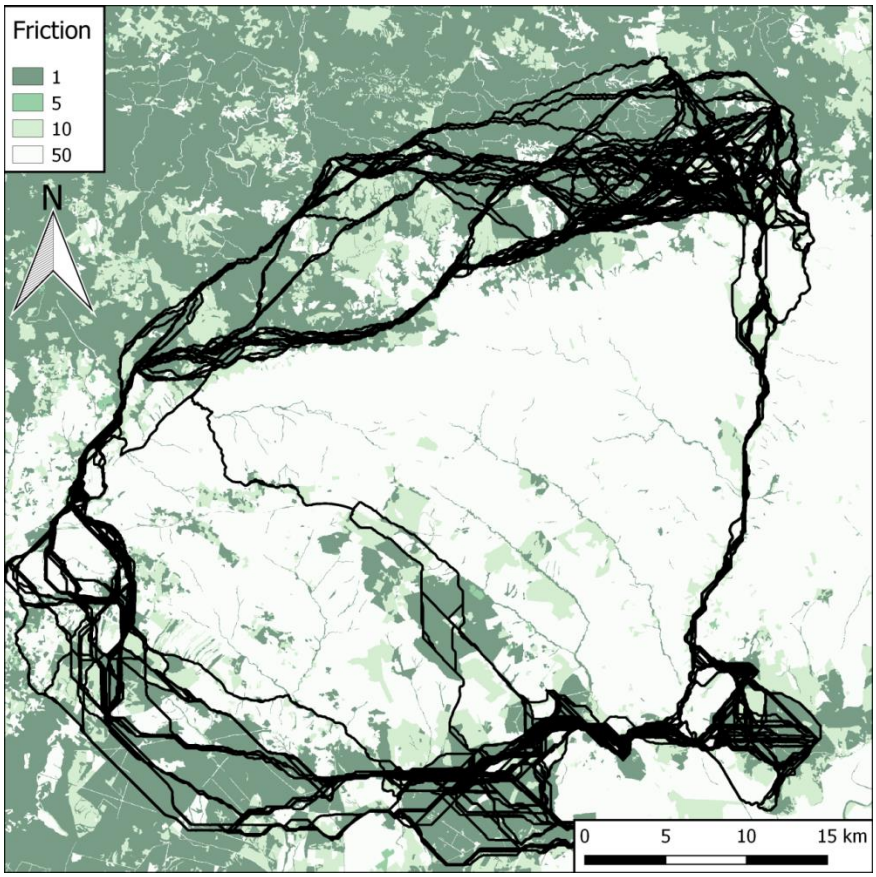


Figure R6 Schematic map representing the concentration of pathways under simulated scenarios. Colour darkness and line type and width represent differences in the frequency of use for potential dispersal. Critical connectivity sites, indicated by arrows, were defined as areas with only one set of possible trajectories.

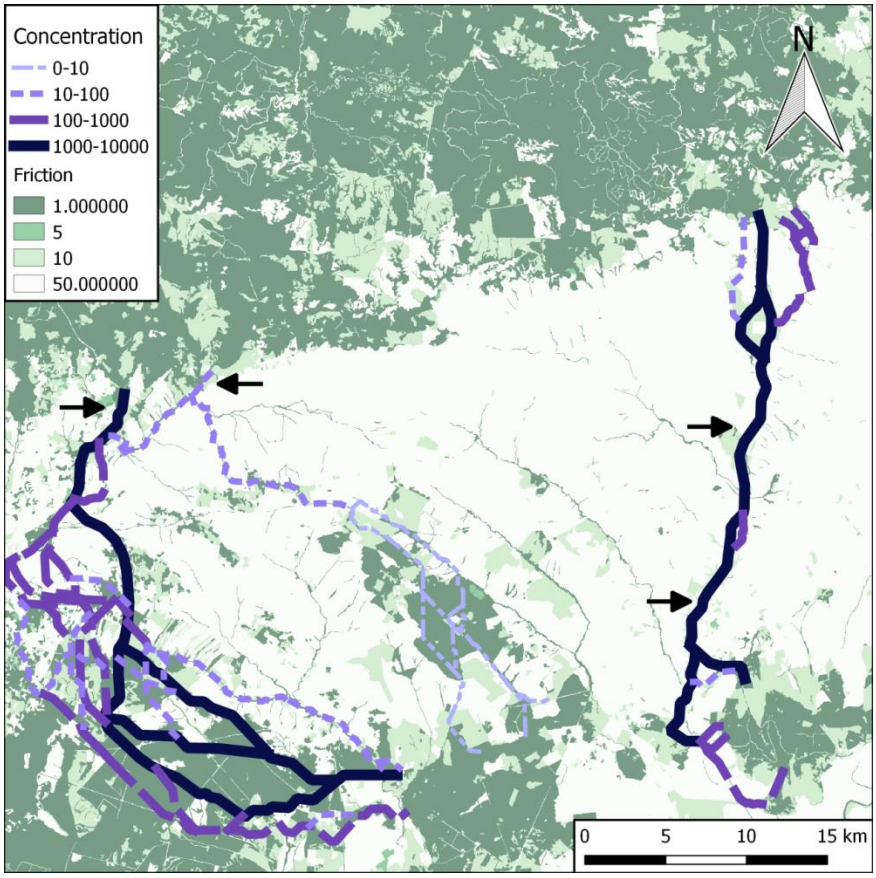
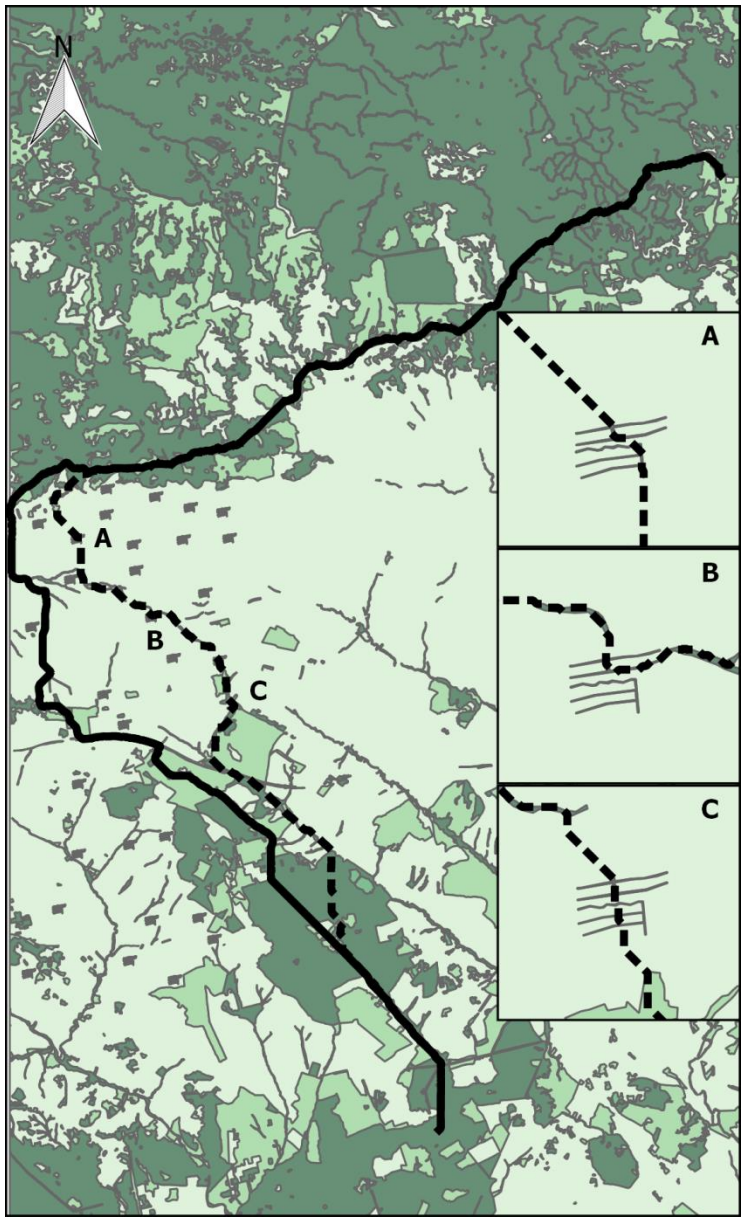


Table R12 Fit indicators for binomial generalized linear models relating the creation of new paths for carnivores between forest landscapes. Predictors were hedgerow location in the agricultural landscape (i. e., landscape width and distance to northern and southern forest landscapes), local landscape context (i. e., the number of habitat patches in a 1-km buffer around hedgerows), and restoration effort (number of restored hedgerows). Coefficients are shown only for models with a good fit, defined by ΔAIC ≤ 2. AIC: Akaike Information Criterion.

Model	AIC	ΔAIC	Effect	Estimate	SE	P
Context + Dist. North + Dist. South + Width + Effort	**32.83**					
			Context	1.355	1.537	0.378
			Dist. North	1.118	1.164	0.337
			Dist. South	-0.491	1.015	0.629
			Width	**-7.680**	**3.894**	**0.049**
			Effort	0.266	0.394	0.499
Width	37.08	4.25				
Context	73.10	40.27				
Dist. North + Dist. South	80.50	47.67				
Effort	83.98	51.15				

Figure R7 One realization of simulations showing the effect of hedgerow restoration on the connectivity of the agroecosystem. As we expected, the restoration of hedgerows promoted the creation of alternative paths across the agroecosystem. In this example, the restoration of three hedgerows (A, B and C) created a new path (thick broken line) as an alternative to the only existing path (solid line).



3.4 The influence of landscape heterogeneity on carnivore occupancy of forest fragments in a Mediterranean agroecosystem

Regarding agroecosystem heterogeneity, differences were consistently higher for all spatial resolutions when the threshold in the proportion of woody cover was 10% (Table R13; Appendix M10.2). We employed this threshold to establish the boundary between the mosaic and simplified landscapes (Figure R8).

Eurasian badger was recorded in 17 fragments, 12 of them in the mosaic landscape (70.6%; incidence = 0.46) and 5 in the simplified landscape (29.4%; incidence = 0.33). Common genet was recorded in 15 fragments, 10 of them in the mosaic landscape (66.7%; incidence = 0.38) and 5 in the simplified landscape (33.3%; incidence = 0.33). Finally, Egyptian mongoose was recorded in 18 fragments, 15 of them in the mosaic landscape (83.3%; incidence = 0.58) and 3 in the simplified landscape (16.7%; incidence = 0.20).

The relative contribution of fragment quality, landscape context and regional connectivity in the selected models varied markedly between the mosaic landscape and the simplified landscape (Table R14, Figure R9; Appendix R3). Fragment occupancy in the mosaic landscape was mainly determined by variables of fragment quality (Figure R9b), whereas the importance of landscape context and regional connectivity increased in the simplified landscape (Figure R9c). The relative importance of both types of effect was intermediate in the entire agroecosystem (Figure R9a). The response of all three species was quite similar in the entire agroecosystem and the mosaic landscape. The occupancy of all species was primarily determined by fragment quality, whereas the relative contribution of landscape context and regional connectivity was smaller. However, very different species-specific responses arose in the simplified landscape.

For the Eurasian badger, summing up the independent contributions of each group of variables in the whole study area, fragment quality contributed nearly half of the explained variance, landscape context contributed the half, and

regional connectivity contributed the remaining 4% (Figure R9a). In the mosaic landscape, fragment quality raised to 88%, whereas landscape context contributed and regional connectivity contributed in a low proportion (Figure R9b). In contrast, in the simplified landscape, landscape context contributed entirely to the explained variance (Figure R9c).

For the genet, summing up the independent contributions of each group of variables in the entire agroecosystem, fragment quality contributed 85% of the explained variance, while landscape context and regional connectivity contributed in a low proportion (Figure R9a). In the mosaic landscape, fragment quality contributed three-quarters of total variance, landscape context contributed 20%, and the regional connectivity contributed a low proportion (Figure R9b). Conversely, in the simplified landscape, only fragment quality contributed to explain variance (Figure R9c).

Finally, in the case of Egyptian mongoose, summing up the independent contributions of each group of variables in the whole study area, fragment quality contributed two-thirds of explained variance, landscape context contributed 19%, and regional connectivity contributed 14% (Figure R9a). In the mosaic landscape, fragment quality contributed 91% and the remaining low proportion was explained by regional connectivity variables (Figure R9b). On the contrary, in the simplified landscape, fragment quality contributed two thirds and regional connectivity contributed the remaining third (Figure R9c).

Table R13 Variation in the number of cells where the proportion of woody cover exceeds different threshold values, at different spatial resolutions. Right panel: difference in the number of cells between adjacent threshold values. The pair of threshold values including large differences for the highest number of spatial resolutions is highlighted in bold.

		Threshold values					Differences between thresholds			
		a 0.10	b 0.15	c 0.20	d 0.25	e 0.30	**a-b**	b-c	c-d	d-e
Spatial resolution	10 km^2	9	8	8	7	6	1	0	1	1
	5 km^2	33	25	23	20	18	8	2	3	2
	2.5 km^2	90	78	71	59	55	12	7	13	4
	1.25 km^2	286	250	220	206	190	36	30	14	16
					Sum of differences		**57**	39	31	23
							3	0	2	1

Figure R8 Allocation of forest fragments to the mosaic landscape (> 10% forest; 26 fragments) and the simplified landscape (≤ 10% forest; 15 fragments). The boundary between the two landscapes is indicated by the broken line.

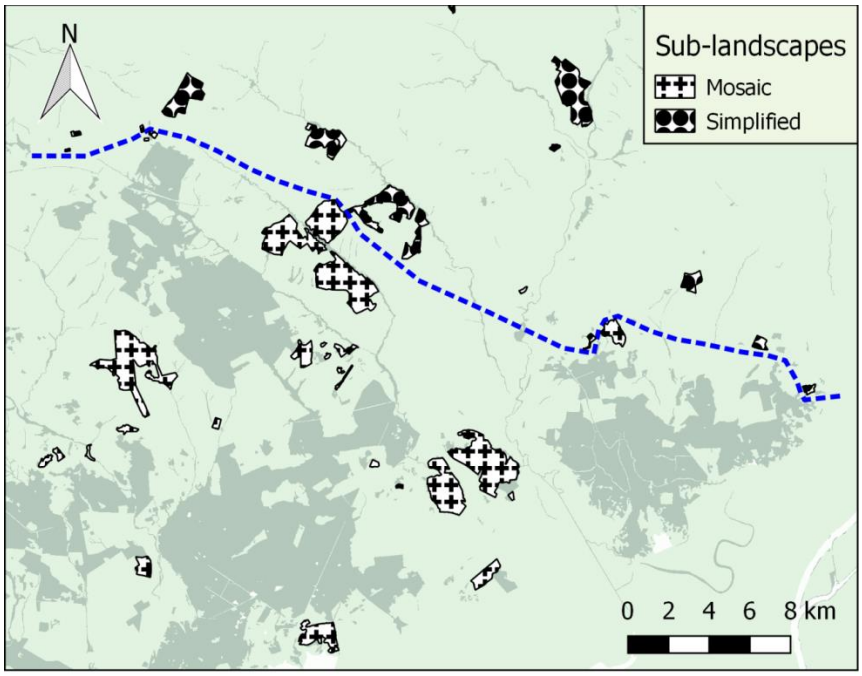


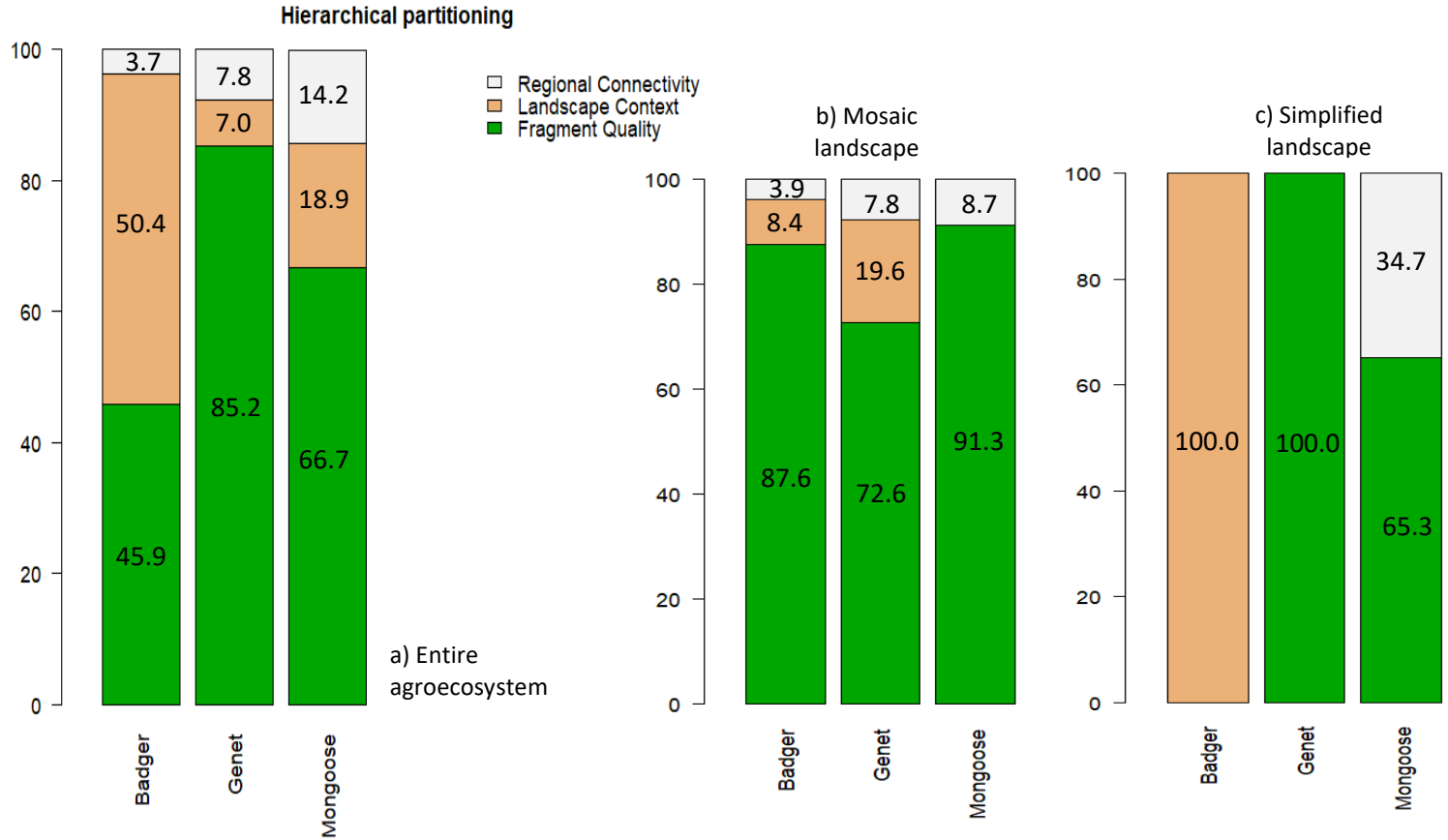
Table R14 Competing models of fragment occupancy for (a) Eurasian badger, (b) common genet and (c) Egyptian mongoose. Occupancy was modelled for the whole agroecosystem, the mosaic landscape, and the simplified landscape. Predictors representing processes at different spatial scales (local, landscape and regional) are shown in different columns. For each model, the values of AICc, and $\Delta_i = AICc_i - AIC_{minc}$, are shown. The sign of the effects for the most parsimonious models is shown in Appendix R3.

Species	Landscape	Model			AICc	Δ_i
		Fragment Quality	**Landscape Context**	**Regional Connectivity**		
(a) *Eurasian badger*	Total	Area + Tree + Habitat Diversity + Disturbances	Linear Elements + Hedge + Dforest	BCPC Area	40.46	
		Area + Tree + Shrub + Habitat Diversity + Disturbances	Linear Elements + Dforest	BCPC Area	40.48	0.02
		Area + Tree + Shrub + Habitat Diversity + Disturbances	Linear Elements + Hedge + Dforest		40.82	0.36
		Tree + Shrub + Habitat Diversity + Disturbances	Linear Elements + Hedge + Dforest	BCPC Area	40.92	0.46
		Area + Tree + Shrub + Disturbances	Linear Elements + Hedge + Dforest	BCPC Area	41.12	0.66
		Area + Tree + Shrub + Habitat Diversity + Disturbances	Linear Elements + Hedge + Dforest	BCPC Area	42.42	1.96
	Mosaic	Tree + Shrub + Disturbances	Hedge + Dforest		26.06	
		Tree + Shrub + Disturbances	Hedge + Dforest	DDNP	26.76	0.70
		Tree + Shrub	Hedge + Dforest	DDNP	27.91	1.85

	Simplified		Linear Elements + Dforest		15.52	
			Linear Elements		16.60	1.08
			Dforest		16.71	1.19
(b) *Common genet*	Total	Area + Tree + Habitat Diversity + Stream	Hedge + Dforest	BCPC Woody Cover	31.96	
		Area + Tree + Shrub + Habitat Diversity + Stream	Dforest	BCPC Woody Cover	33.25	1.29
		Area + Tree + Shrub + Habitat Diversity + Stream	Hedge	BCPC Woody Cover	33.50	1.53
		Area + Tree + Shrub + Habitat Diversity + Stream	Hedge + Dforest	BCPC Woody Cover	33.77	1.80
	Mosaic	Tree + Habitat Diversity + Stream	Dforest	DDNP	26.40	
		Tree + Habitat Diversity + Stream	Hedge + Dforest		26.56	0.16
		Tree + Stream	Hedge + Dforest	DDNP	26.65	0.25
		Tree + Habitat Diversity + Stream	Hedge	DDNP	27.66	1.27
		Tree + Habitat Diversity + Stream	Hedge + Dforest	DDNP	28.27	1.88

	Simplified	Area + Shrub			13.16	
(c) *Egyptian mongoose*	Total	Shrub + Habitat Diversity + Stream + Disturbances	Linear Elements + Hedge	DDNP + BCPC Woody Cover	31.35	
		Area + Habitat Diversity + Stream + Disturbances	Linear Elements + Hedge	DDNP + BCPC Woody Cover	31.67	0.32
		Area + Shrub + Habitat Diversity + Stream + Disturbances	Linear Elements + Hedge	DDNP + BCPC Woody Cover	33.33	1.98
	Mosaic	Habitat Diversity + Stream + Disturbances		BCPC Woody Cover	22.71	
		Habitat Diversity + Stream + Disturbances			24.35	1.64
	Simplified	Disturbances		DDNP	15.05	
		Disturbances			16.74	1.69

Figure R9 The relative contribution of fragment quality, landscape context and regional connectivity for each species and landscape. Different relative contributions were found between the mosaic and the simplified landscapes. In the mosaic landscape (b) occupancy was primarily determined by fragment quality variables, whereas the importance of landscape context and regional connectivity increased in the simplified landscape (c). The relative contribution of landscape and regional variables was qualitatively similar between species in the entire agroecosystem (a) and the mosaic landscape (b). However, in the simplified landscape (c), we found marked species-specific differences in the relative importance of each type of predictor.


Hierarchical partitioning
Regional Connectivity
Landscape Context
Fragment Quality
100
80
60
40
20
0
3.7
50.4
45.9
7.8
7.0
85.2
14.2
18.9
66.7
Badger
Genet
Mongoose
a) Entire agroecosystem
b) Mosaic landscape
3.9
8.4
87.6
7.8
19.6
72.6
8.7
91.3
c) Simplified landscape
100.0
100.0
34.7
65.3

3.5 Regional and local processes of mesocarnivore community assembly in an agroecosystem surrounded by Mediterranean forest

We recorded eight carnivore species throughout the study period (Table R15). Differences between species in mean distance travelled per day are shown in Table R16 and Appendix R4. Mean dispersal distances of the European polecat (*Mustela putorius*) and the common genet (*Genetta genetta*) were significantly lower than those of the other species, whereas mean dispersal distances of the wildcat (*Felis silvestris*) and the red fox (*Vulpes vulpes*) were significantly higher than those of the other species. Differences in dispersal distances among the other four species were low (Table R16). Dispersal ability was not correlated with how widespread the species were distributed in the study area. For example, the Egyptian mongoose, the European polecat and the common genet, which travelled short distances per day (Appendix R4), were recorded in all three landscapes. Conversely, the wildcat, which is able to cover long dispersal distances, was bound to the forest landscape of Sierra Morena (Table R15). Species as the red fox, the Eurasian otter, the stone marten and the Eurasian badger showed similar dispersal distances (Table R16). Nevertheless, whereas Eurasian badger and red fox were recorded in all three landscapes, stone marten was restricted to Sierra Morena and, the Eurasian otter was absent in the Doñana forest landscape.

Spatial analyses discriminated 15 spatial structures across the study area. The highest order PCNM described approximately the separation of sampling units in Sierra Morena from sampling units elsewhere (Figure R10, PCNM1). Subsequent high order PCNMs distinguished part of the agroecosystem and western units in both Sierra Morena and Doñana forest landscapes (Figure R10, PCNM2) and the separation of the three landscapes (Figure R10, PCNM3). Structures represented by low order PCNMs reveal less evident spatial patterns; the finer the scale of spatial structures, the harder to interpret (Figure R10; PCNM6, PCNM10).

Differences in species composition

Mean (± SD) species richness in Sierra Morena (6.13 ± 1.25) was higher than in the agroecosystem (4.00 ± 1.69) and the Doñana forest landscape (4.13 ± 0.35). Species richness differed significantly between the three landscapes (F = 7.52, df = 2, P = 0.003). Specifically, the species richness of Sierra Morena forest landscape differed significantly from the species richness found in the agricultural landscape (95% CI [0.58 – 3.67]) and the Doñana forest landscape (95% CI [0.45 – 3.55]), but no significant differences in species richness were found between the agricultural landscape and Doñana (95% CI [-1.42 – 1.67]). Nestedness among sites was greater than expected by chance (NODF = 84.28, P = < 0.01, SES = 3.20). The regional species pool was fully represented in Sierra Morena (SM1-8, Figure R10), whereas Doñana (DNR 1-8) and the agroecosystem (AGR 1-8) harboured only a subset of species (Figure R11). The homogeneity of species composition in Doñana was notable, with six of the eight sampling units (DNR 2, 4-8) occupied by the same four mesocarnivore species: red fox, common genet, Egyptian mongoose and Eurasian badger (Figure R11).

Jaccard's multiple-site dissimilarity (JI_T = 0.86) was associated to species replacement (turnover dissimilarity component; JI_{TU} = 0.64, 74% of total index) more than to the spatial pattern of species loss (nested dissimilarity component; JI_{NE} = 0.22, 26% of total index). Redundancy analysis showed that adjusted R^2 for the turnover dissimilarity component (R^2_a = 0.64) was higher than for the nestedness component (R^2_a = 0.30), whereas adjusted R^2 for total dissimilarity showed an intermediate value (R^2_a = 0.46). Total dissimilarity was explained by a combination of spatial, environmental and spatially autocorrelated environmental variables (Figure R12A), where most of the variance was accounted for by the joint effects of space and environmental variables. Nested dissimilarity was explained by a combination of spatial and spatially autocorrelated environmental variables (Figure R12B). Turnover dissimilarity was fully explained by environmental variables. Specifically, a combination of local and landscape environmental variables explained the variation in species

composition related to species replacement (Figure R12C). Total dissimilarity analysis yielded a combination of the results obtained for nestedness and turnover components (Figure R12).

Individual contributions of spatial and environmental variables explaining the nestedness dissimilarity component showed that the spatial fraction was represented by a large-scale spatial structure (PCNM3) and an intermediate spatial structure (PCNM6; Table R17b). The mean proportion of scrubland at the macrohabitat scale was a local variable affecting the spatial pattern of ordered species loss. Indeed, we found significant differences in the mean proportion of shrubland cover (%) at the macrohabitat scale (χ^2 = 10.15, df = 2, P = < 0.01) between landscapes. A post hoc Tukey test showed that the Sierra Morena forest landscape and the agricultural landscape differed significantly at $p < 0.05$. These differences described a drastically decrease in the proportion of shrubland cover from Sierra Morena (mean = 59.9%, SD = 28.6%), to the agricultural landscape (mean = 2.7%, SD = 3.3%). Landscape variables attributable to the nestedness component were not retained in final models of species composition.

The spatial structure did not contribute to explain variation in the turnover component of dissimilarity in species composition (Table R17c). Local variables, represented by the mean cover of open habitat at the microhabitat scale, and forest availability in the landscape context of sampling units, explained the variation in species composition associated with species replacement.

For total dissimilarity, we found a combination of the type predictors relevant to explain the nestedness and turnover components of dissimilarity. The spatial fraction was primarily represented by large-scale spatial structures: PCNM1, PCNM2 and PCNM3 (Table R17a). However, PCNM6 and PCNM10, from intermediate and fine-scale spatial structures, respectively, also contributed significantly to explain variation in species composition. The local fraction of environmental variables was represented by the mean cover of open habitat at

the microhabitat scale, human disturbance expressed in terms of dog activity, and the proportion of riparian vegetation at the macrohabitat scale. The landscape fraction was represented by the proportion of scrubland in the landscape context.

We show spatial autocorrelation patterns for the environmental variables explaining dissimilarity in Figure R13. Spatial autocorrelation was significantly higher than expected for the mean cover of open habitat (Moran's I = 0.26, SD = 0.05, P < 0.01), the proportion of riparian vegetation at the macrohabitat scale (Moran's I = 0.16, SD = 0.05, P < 0.01), the proportion of scrubland at the macrohabitat scale (Moran's I = -0.04, SD = 0.05, P = 0.07) and the proportion of scrubland in the landscape context (Moran's I = 0.15, SD = 0.05, P < 0.01), whereas it was not significantly different for dog activity (Moran's I = -0.04, SD = 0.05, P = 0.92). Comparing spatial structures (i. e. PCNMs) with spatial patterns of autocorrelation, we found spatial autocorrelation between the PCNM6 and dog activity (Figure R13B); between PCNM1 and the proportion of shrubland cover in the landscape context (Figure R13E); and a weak spatial autocorrelation between PCNM3 and the proportion of shrubland at the macrohabitat scale (Figure R13D).

Species co-occurrence

Co-occurrence analyses described a non-significant trend toward segregation of mesocarnivore species (C-Score = 0.69, P = 0.057, SES = 1.81).

Table R15 Matrix of mesocarnivore occurrence in the three landscapes: the forest landscape of Sierra Morena (SM), the more heterogeneous forest landscape of the Doñana Nature Reserve (DNR), and the agroecosystem (AGR). Occurrence (1) indicates that the species was recorded in at least one sampling period, whereas absence (0) means that the species was not detected by any method throughout the study years. Numbers in the first column refer to spatial replicates within each landscape.

	Vulpes vulpes	*Felis silvestris*	*Herpestes ichneumon*	*Lutra lutra*	*Martes foina*	*Meles meles*	*Mustela putorius*	*Genetta genetta*
SM1	1	1	1	1	1	1	1	1
SM2	1	1	1	1	0	1	0	1
SM3	1	0	1	1	1	1	0	1
SM4	1	0	1	1	0	1	0	1
SM5	1	1	1	1	1	1	0	1
SM6	1	1	1	1	1	1	0	1
SM7	1	0	1	1	1	1	0	1
SM8	1	0	1	1	0	1	0	0
DNR1	1	0	1	0	0	0	1	1
DNR2	1	0	1	0	0	1	0	1
DNR3	1	1	1	0	0	1	0	1
DNR4	1	0	1	0	0	1	0	1
DNR5	1	0	1	0	0	1	0	1
DNR6	1	0	1	0	0	1	0	1
DNR7	1	0	1	0	0	1	0	1
DNR8	1	0	1	0	0	1	0	1
AGR1	1	1	0	1	0	1	0	0
AGR2	1	0	0	1	0	0	0	0
AGR3	1	0	0	1	0	0	0	0
AGR4	1	0	0	1	0	0	0	1
AGR5	1	0	1	1	0	1	0	1
AGR6	1	0	1	1	0	1	0	1
AGR7	1	0	1	1	0	0	0	1
AGR8	1	1	1	1	0	1	1	1

Table R16 Differences between carnivore species in distance travelled during dispersal (Km/day) expressed as correlation coefficients (r) derived from Cohen's d transformation (Cohen 1988). Paired comparisons with r > 0.371 represent species with different movement capacity. The sign of coefficients indicates differences between species in distance travelled during dispersal. Positive signs indicate that species in row shows higher distance travelled during dispersal (lower if the sign is negative). Significant correlation coefficients are highlighted in bold.

	Felis silvestris	*Herpestes ichneumon*	*Lutra lutra*	*Martes foina*	*Meles meles*	*Mustela putorius*	*Genetta genetta*
Vulpes vulpes	**-0.580**	**0.890**	0.080	0.222	**0.491**	**0.935**	**0.721**
Felis silvestris		**0.882**	**0.443**	**0.552**	**0.745**	**0.925**	**0.817**
Herpestes ichneumon			**-0.487**	**-0.438**	**-0.921**	**0.880**	0.039
Lutra lutra				0.096	0.125	**0.699**	**0.453**
Martes foina					0.000	**0.694**	**0.399**
Meles meles						**0.945**	**0.616**
Mustela putorius							**-0.583**

Figure R10 Sketch of the study are showing sampling units (squares) and a subset of different Principal Coordinates of Neighbour Matrices (PCNMs) that were included in competitive models of dissimilarity in species composition (Table R17). PCNMs represent a continuum of spatial structures among sites, where high order spatial variables (PCNM1, PCNM2, PCNM3) reveal large-scale variation among sites, and low order spatial variables (PCNM10) indicate very fine-scale spatial variation among sites. In PCNM panels shades identify sampling units belonging to the same structure. The lower right panel shows the identification code of sampling units. Background colours outline the limits of the three landscapes. Longitude and latitude were expressed as significant figures of the UTM projection (zone 30N).

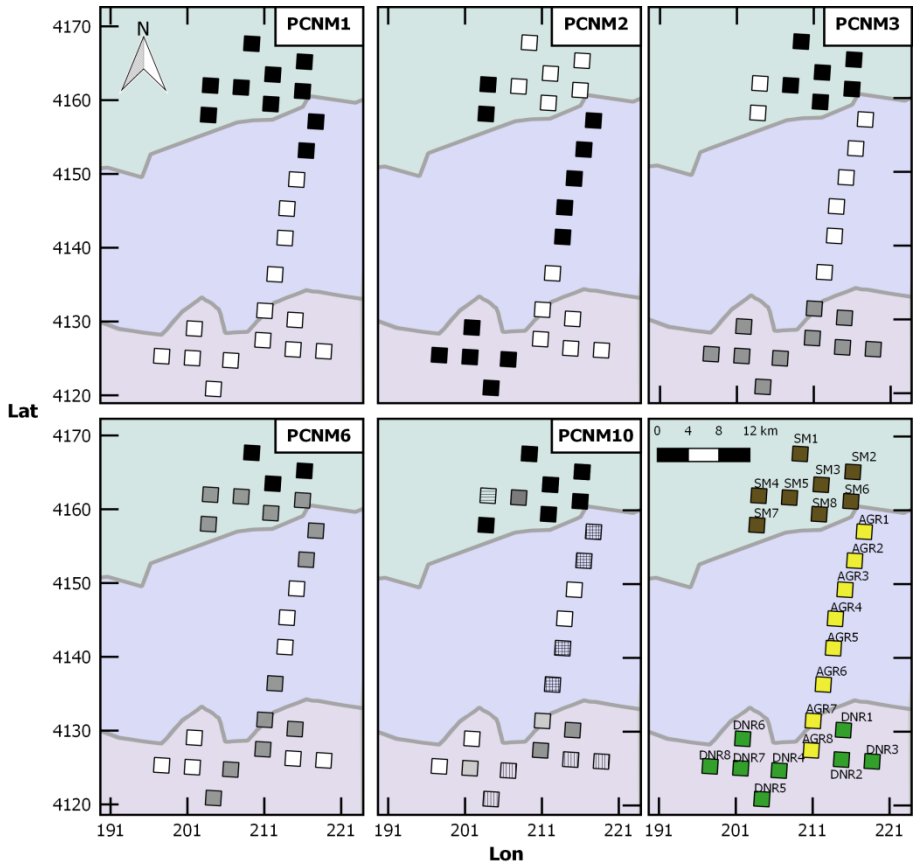

PCNM1
PCNM2
PCNM3
PCNM6
PCNM10
N
0 4 8 12 km
SM1
SM2
SM3
SM4
SM5
SM6
SM7
SM8
AGR1
AGR2
AGR3
AGR4
AGR5
AGR6
AGR7
AGR8
DNR1
DNR2
DNR3
DNR4
DNR5
DNR6
DNR7
DNR8
Lat
Lon
4170
4160
4150
4140
4130
4120
191
201
211
221

Figure R11 Matrix of sample landscapes (rows, Figure R10) ordered by mesocarnivore species richness. Species composition fits a clear nested pattern where communities in the Doñana forest landscape (DNR) and the agricultural landscapes (AGR) tend to be ordered subsets of communities in the Sierra Morena forest landscape (SM). Perfect nestedness is represented by the matrix diagonal (Atmar and Patterson 1993), which defines unexpected absences (white cells above the line) and unexpected presences (red cells below the line).

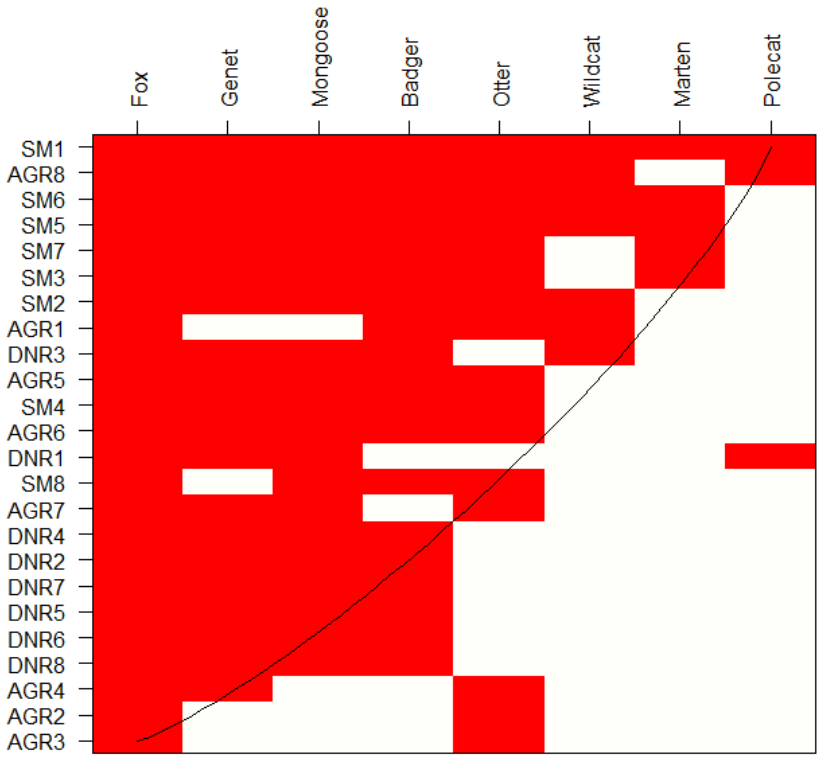


Figure R12 The relative contribution of spatial variables, environmental variables and spatially autocorrelated environmental variables to explain variation in mesocarnivore species composition in a Mediterranean agroecosystem surrounded by forest landscapes. Numbers denote the percentage of variation in dissimilarity explained by each type of variables. This contribution was measured for total dissimilarity as well as for nestedness and turnover dissimilarity components (Baselga 2010). Variation in the turnover component of dissimilarity (Panel C) was explained only by environmental variables which were broken down into local and landscape variables.

A) Total dissimilarity

B) Nestedness component

C) Turnover component

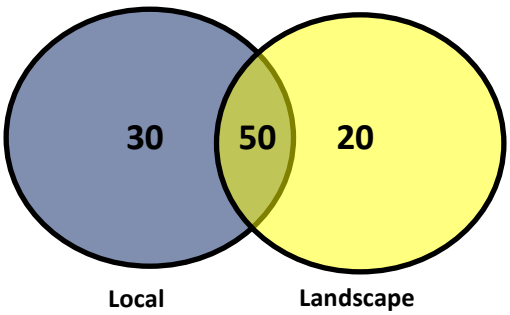
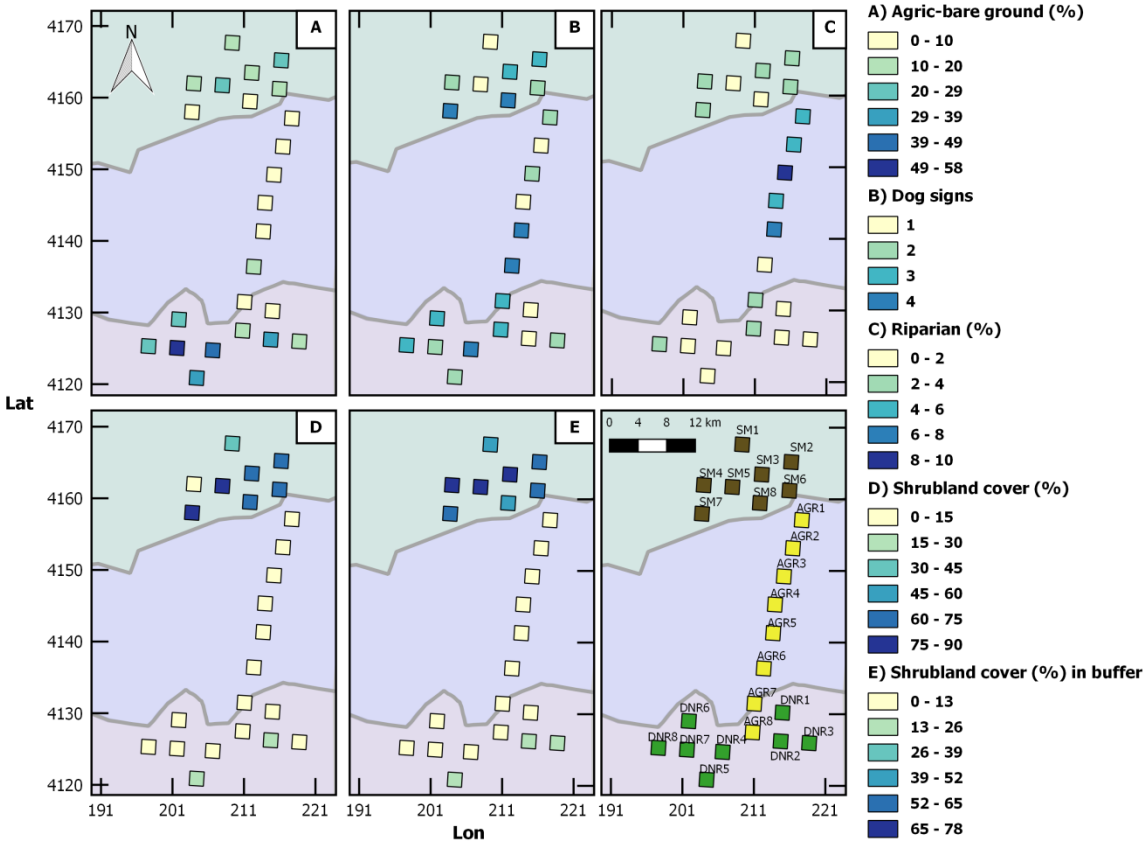


Table R17 Factors explaining differences in mesocarnivore species composition in a Mediterranean agroecosystem surrounded by forest landscapes. We show the contribution of individual variables for total dissimilarity, nestedness component, and turnover component from redundancy models refit after dissimilarity randomisation. The total sum of squares represents distance-based RDA total variation (explained and non-explained), whereas the sum of squares represents only the individual effect of each variable. We also highlight the proportion of total explained variation accounted for each variable.

Dissimilarity	Total Sum of Squares	Adjusted R^2	Variables	Sum of Squares	Expl. Var. (%)	Pseudo-F	P
a) Total	4.53	0.46					
			PCNM1	0.91	29.84	8.62	< 0.01
			PCNM2	0.32	10.49	3.04	0.01
			PCNM3	0.36	11.80	3.40	< 0.01
			PCNM6	0.41	13.44	3.91	< 0.01
			PCNM10	0.29	9.51	2.73	0.02
			Crops/bare	0.16	5.25	1.48	0.18
			Dog	0.22	7.21	2.07	0.06
			Riparian	0.16	5.25	1.54	0.15
			ShrubB	0.20	6.56	1.93	0.07
b) Nested	2.85	0.30					

			PCNM3	0.69	62.16	7.95	< 0.01
			PCNM6	0.32	28.83	3.73	0.03
			Shrub	0.10	9.01	1.10	0.34
c) Turnover	1.68	0.64					
			Crops/bare	0.38	33.93	27.81	< 0.01
			CanopyB	0.74	66.07	14.28	< 0.01

Figure R13 Spatial autocorrelation patterns of environmental variables explaining variation in species composition, in terms of total dissimilarity and nestedness component. The environmental variables represented are A) the mean crop and bare ground cover (%), B) the standardized relative abundance of dog signs, C) the proportion of riparian cover (%), D) the proportion of scrubland (%), and E) the proportion of scrubland (%) in a 1-km buffer around the sampling units. The lower right panel shows the identification code of sampling units. Background colours outline the limits of the three landscapes. Longitude and latitude were expressed as significant figures of the UTM projection (zone 30N).


A
B
C
D
E
N
Lat
Lon
4170
4160
4150
4140
4130
4120
191
201
211
221
0 4 8 12 km
SM1
SM2
SM3
SM4
SM5
SM6
SM7
SM8
AGR1
AGR2
AGR3
AGR4
AGR5
AGR6
AGR7
AGR8
DNR1
DNR2
DNR3
DNR4
DNR5
DNR6
DNR7
DNR8
A) Agric-bare ground (%)
0 - 10
10 - 20
20 - 29
29 - 39
39 - 49
49 - 58
B) Dog signs
1
2
3
4
C) Riparian (%)
0 - 2
2 - 4
4 - 6
6 - 8
8 - 10
D) Shrubland cover (%)
0 - 15
15 - 30
30 - 45
45 - 60
60 - 75
75 - 90
E) Shrubland cover (%) in buffer
0 - 13
13 - 26
26 - 39
39 - 52
52 - 65
65 - 78

Appendix R1 Comparison of generalised linear mixed models of mammal detection.

The null model contains a single factor, either Landscape or Season, depending on the species. Other models considered also include the main effect of lure type (factor Type), its interaction with Landscape or Season, and the interaction between Type and covariates potentially affecting visibility. Only models with good fit, defined by $\Delta AIC \leq 2$, are shown, and parameter estimates are deployed only for selected models containing significant effects. AIC: Akaike Information Criterion. w_i: Akaike weights.

Species	Model	AIC	ΔAIC	w_i	Effect	Estimate	SE	P
Oryctolagus cuniculus	Landscape + Type + Cover	1136.9		0.864				
					Visual	-0.043	0.22	0.840
					Auditory	-0.532	0.24	0.028
					Cover	-3.092	0.57	<0.001
Lepus granatensis	Landscape	280.54		0.757				
Vulpes vulpes	Landscape + Type	520.33		0.499				
					Visual	-0.793	0.39	0.043

					Auditory	-1.287	0.48	0.007
	Landscape + Type*Cover	521.04	-0.70	0.352				
					Visual	-0.837	0.69	0.223
					Auditory	-2.360	1.01	0.019
					Cover	-1.588	0.83	0.057
					Visual* Cover	0.223	1.86	0.905
					Auditory* Cover	2.897	1.95	0.138
Genetta genetta	Season + Type	427.87		0.517				
					Visual	0.890	0.36	0.014
					Auditory	0.219	0.43	0.609
	Season*Type	428.96	-1.09	0.299				
Herpestes ichneumon	Season	174.63		0.988				

Appendix R2 The effect of survey method on detection. We show the coefficients and significance of the predictors in generalised linear mixed models with error and sampling plot as the random effect. Survey methods were compared against the method included in the intercept, which was camera traps for all species but red deer, wild boar, Eurasian otter, stone marten and Iberian lynx (scat surveys) and wildcat (scent stations). Models for the common genet did not converge and are not shown.

Species	Methods	Estimate	SE	P
O. cuniculus				
	Scent stations	2.224	0.379	< 0.001
	Track surveys	3.960	0.463	< 0.001
	Scat surveys	3.960	0.463	< 0.001
L. granatensis				
	Scent stations	1.512	0.591	0.011
	Track surveys	2.897	0.586	< 0.001
	Scat surveys	3.153	0.589	< 0.001
C. elaphus				
	Track surveys	2.225	0.637	< 0.001
S. scrofa				
	Track surveys	1.554	0.247	0.004
V. vulpes				
	Scent stations	2.272	0.522	< 0.001
	Track surveys	4.835	0.570	< 0.001
	Scat surveys	3.952	0.537	< 0.001
H. ichneumon				
	Scent stations	0.208	0.646	0.748
	Track surveys	3.320	0.572	< 0.001
	Scat surveys	-0.562	0.765	0.462

M. meles				
	Scent stations	1.866	1.094	0.088
	Track surveys	4.241	1.039	< 0.001
	Scat surveys	1.430	1.131	0.206
L. lutra				
	Track surveys	-1.451	-3.432	< 0.001
M. putorius				
	Scent stations	< 0.001	1.505	1.000
	Track surveys	0.828	1.332	0.534
	Scat surveys	0.828	1.332	0.534
M. foina				
	Track surveys	-2.640	1.166	0.024
L. pardinus				
	Track surveys	< 0.001	1.194	1.000
F. silvestris				
	Track surveys	2.156	1.071	0.044

Appendix R3 Selected models of fragment occupancy models for Eurasian badger, common genet and Egyptian mongoose in the whole agroecosystem, the mosaic landscape (>10 % woody cover) and the simplified landscape (<10 % woody cover). Significant effects are typed in bold. The independent variance explained by each variable was calculated by means of hierarchical partitioning.

Species	Landscape	Variables	Estimator	SE	P	Independent variance (%)
(a) Eurasian badger	(1) Total	Area	-0.37	0.51	0.44	1.71
		Tree	0.64	0.50	0.15	17.78
		Shrub	0.20	0.48	0.68	3.53
		LU Diversity	0.35	0.47	0.43	1.53
		Disturbances	**-2.07**	**1.07**	**0.03**	**21.35**
		Linear Elements	**1.81**	**1.03**	**0.04**	**29.16**
		Hedge	0.15	0.47	0.75	1.85
		Dforest	**-0.66**	**0.44**	**0.04**	**19.35**
		BCPC Area	0.56	0.46	0.28	3.73
	(2) Mosaic	**Tree**	**1.16**	**0.71**	**0.04**	**31.11**
		Shrub	**1.51**	**0.75**	**0.01**	**22.70**
		Disturbances	**-2.43**	**1.33**	**0.03**	**33.82**
		Hedge	1.07	0.70	0.07	8.44
		DDNP	-0.96	0.77	0.15	3.94

	(3) Simplified	**Linear Elements**	**3.60**	**1.79**	**0.02**	**68.74**
		Dforest	-0.92	0.72	0.07	31.27
(b) Common genet	(1) Total	Area	0.61	0.50	0.17	19.91
		Shrub	-0.01	0.52	0.98	3.60
		Habitat Diversity	-1.05	0.64	0.06	8.57
		Stream	**4.36**	**1.83**	**< 0.01**	**53.09**
		Hedge	0.45	0.48	0.32	4.79
		Dforest	-0.32	0.40	0.32	2.23
		BCPC Woody Cover	**1.00**	**0.58**	**0.02**	**7.82**
	(2) Mosaic	**Tree**	**1.42**	**0.72**	**0.01**	**30.00**
		Habitat Diversity	-0.76	0.67	0.25	6.97
		Stream	**2.72**	**1.44**	**0.02**	**35.64**
		Hedge	0.77	0.76	0.29	7.04
		Dforest	0.61	0.62	0.18	12.60
		DDNP	0.73	0.66	0.24	7.75
	(3) Simplified	**Area**	**3.66**	**2.11**	**< 0.01**	**45.84**
		Shrub	**4.38**	**2.50**	**< 0.01**	**54.16**
(c) Egyptian Mongoose	(1) Total	Area	-2.60	1.70	0.14	11.00
		Shrub	0.43	0.54	0.37	2.25
		Habitat Diversity	**2.17**	**1.13**	**0.03**	**3.77**
		Stream	**4.82**	**2.56**	**0.02**	**25.66**

	Disturbances	**-8.96**	**4.22**	**< 0.01**	**24.00**
	Linear Elements	**4.56**	**2.45**	**0.02**	**16.40**
	Hedge	2.02	1.20	0.06	2.54
	DDNP	**-4.34**	**2.08**	**< 0.01**	**11.83**
	BCPC Woody Cover	**-1.34**	**0.79**	**0.04**	**2.33**
(2) Mosaic	**Habitat Diversity**	**6.77**	**4.60**	**0.02**	**7.42**
	Stream	**7.01**	**4.08**	**< 0.01**	**52.55**
	Disturbances	**-13.34**	**8.42**	**< 0.01**	**31.36**
	BCPC Woody Cover	-2.56	1.64	0.06	8.67
(3) Simplified	**Disturbances**	**-5.08**	**2.89**	**0.02**	**65.26**
	DDNP	**-2.34**	**1.55**	**0.04**	**34.74**

Appendix R4 Measures of movement ability of selected carnivore species occurring in the study area. Movement ability is estimated by the mean distance travelled during daily movements, expressed as km per day, of mesocarnivores. Data were extracted from published studies carried out in Mediterranean landscapes, if available; otherwise from any other ecosystems. Mean values were calculated for the highest distances reported in each study.

Species	Km per day	N	Mean Km per day (± SD)	References
Vulpes vulpes	2.0 - 20.0	4	5.9 ± 1.1	Travaini et al. 1993
Felis silvestris	4.2 - 12.1	4	8.2 ± 2.0	Stahl et al. 1988; Palomo et al. 2007
Herpestes ichneumon	0.6-6.4	1	2.9 ± 0.0	Delibes and Beltrán 1985
Lutra lutra	0.8 - 14.2	7	5.5 ± 3.3	Ruiz-Olmo et al. 1995
Martes foina	1.5 - 5.3	52	4.9 ± 2.9	Genovesi et al. 1997
Meles meles	3.9 - 5.5	3	4.9 ± 0.6	Rosalino et al. 2005
Mustela putorius	0.0 - 2.6	3	0.8 ± 0.8	Palazón et al. 2010
Genetta genetta	0.9 - 6.6	8	2.8 ± 1.8	Palomares and Delibes 1994

4. Discussion

In this section, we first discuss the results obtained by each of the studies addressed in this thesis, and then the main contributions derived from them.

4.1 Detection of Iberian terrestrial mammals employing olfactory, visual and auditory attractants

There is a wealth of literature addressing the response of mammals to different lures, often seeking a substance that selectively attracts or is consumed by only one species. With some exceptions (Hanke and Dickman 2013), a single attractant seldom stands out in efficiency or selectivity among the substances compared (e.g. Ausband et al. 2011; Tanner and Zimmerman 2012; Snow and Andelt 2013). This may arise in part because species response to lures has not always been isolated from major confounding factors affecting visiting or trapping rates. The efficiency of mammal detection may vary, for example, with weather and other variables fluctuating seasonally (Mitchell and Kelly 1992; Bubela et al. 1998), the spatial distribution of resources (Short et al. 2002; Moseby et al. 2011) and landscape structure (Graham et al. 2012). The patterns of lure performance we found cannot be attributed to variation in the detection method, landscape structure, or habitat quality, which were offset through balanced sampling in the study design. We can also rule out spatial, seasonal and inter-annual variability in mammal abundance and behaviour, as these factors were controlled for statistically before examining the effect of lures on detection.

Using olfactory attractants, we detected mammals across landscapes with quite different composition and structure, and during seasons differing markedly in species abundance (Beltrán 1991; Coman et al. 1991; Matos et al. 2009). Therefore, the scents we employed may be functional in a variety of ecological conditions. Further, using scents we were able to detect most species of larger mammals known to be present in the study area through independent methods (sign surveys; Rodríguez and Delibes 2003), even species occurring at low densities (authors, unpublished data). We failed to detect only two species,

namely the Eurasian otter (*Lutra lutra*) which is associated to freshwater habitats where detection plots were rarely placed, and the Iberian lynx (*Lynx pardinus*) which was extremely rare in the southern end of the study area during the study period; our sampling units overlapped only one empty lynx territory and some dispersal habitat (Palomares et al. 2003). Therefore, the non-detection of these species cannot be attributed to poor scent performance. For the six species detected less than ten times, three seemed to be very scarce in the lower Guadiamar basin on the basis of sign surveys (European polecat, wildcat and stone marten). Therefore, our results regarding their response to the scents FAS and catnip are inconclusive. In order to tease apart the relative effects of species abundance and scent attraction, further tests should be done in areas where these three species are more abundant. The other three species (Eurasian badger, red deer and wild boar) were not rare at least in some sampling units of one landscape. Although these species were detected, the mismatch between their presumed abundance and detection frequency suggests that they may not be especially responsive to the scents we used.

The small size of sand surfaces and pressure plates, as well as their placement outside travelled routes, made chance detections of animals simply passing very unlikely. Inferring mammal behaviour from pictures helps to further assess actual lure effectiveness, but single photographs have less utility than videos to confirm specific reactions to the attractant at the detection plot. Yet, body position in most pictures corroborated that the two scents we employed elicited investigative behaviour in carnivores. Although this reaction was less apparent, lagomorphs were attracted to scented detection plots, as it has been found elsewhere (Drew et al. 1988). The FAS scent was originally developed for coyote *Canis latrans* management (Roughton and Sweeny 1982), and has been widely used to lure many other mammal species (Andelt and Woolley 1996; Monterroso et al. 2011; Webster et al. 2016). Catnip has been used mainly to attract domestic cats and other felines (Clapperton et al. 1994; McDaniel et al. 2000). Our results confirm that these olfactory lures may be useful to detect not

only carnivores of different families but also species of other mammal orders such as lagomorphs.

The red fox avoided plots where visual or acoustic supplements were added to the scent. The common genet visited plots with scent and visual lures more than expected, but this effect was inconsistent because tinsel strips were also present in plots with acoustic lures and these plots were not visited more than expected. An aversive reaction to one or both of the non-olfactory attractants, perhaps occurring only under specific circumstances, could be an explanation that should be tested by assessing the performance of visual and acoustic lures separately. Novel objects may provoke neophobia in wild mammals (Sunnucks 1998), especially in canids (Travaini et al. 2013; Moretti et al. 2015). The attraction of scents may help these species to overcome their distrust towards recording devices, such as scent stations or cameras, which may also be perceived as novel objects (Harris and Knowlton 2001). However, the visual and acoustic lures we employed are additional structures that could have counteracted this effect, thus inducing neophobic behaviour in some species.

The experimental design did not allow us to rule out indifference, or even repulsion, to scents as a potential cause for low detection frequency of six mammal species. As a reference for FAS we can use species preferences reported for several carnivore species in captivity by Monterroso et al. (2011). The wildcat exhibited little response to FAS in captivity and even catnip may not be invariably efficient in attracting felines such as feral cats (Hanke and Dickman 2013). Captive stone martens showed a marked positive response to FAS which would predict detection frequencies higher than observed in our study. On the other hand, some inconsistencies between the response of captive animals and their wild conspecifics become apparent and blur the patterns of scent attraction for some species. For example, stone martens did not show preference for lynx urine in captivity but responded to this lure in the field (Monterroso et al. 2011), whereas captive red foxes exhibited a weak response to FAS that is at odds with the regular detection of wild foxes in FAS-scented plots during the present study. For wildcat, stone marten and European polecat,

the hypothesis of a limited response to FAS and catnip is not rejected but it seems less parsimonious to explain low detection frequency than the hypothesis of species scarcity. Indifference to scents might be more likely as an explanation for low detection frequency in common species such as the Eurasian badger which also showed reduced investigative behaviours towards other attractants in the experiments conducted by Monterroso et al. (2011). In the case of wild ungulates, avoidance of scents or, more likely, of the combined set of attractant-detection device could have played a role.

We found that the addition of visual and acoustic lures to scents did not generally improve detection rates for most species, in agreement with previous field studies (Gabor et al. 1994; Chamberlain et al. 1999; Molsher 2001; Cove et al. 2014; Read et al. 2015). Employing extra attractants increases the cost of surveys. In the case of wooden bells, the cost was one order of magnitude higher than that of scents and visual lures. Moreover, we found some disparity in the response of species to different lures; in particular, some species tended to avoid plots with visual or acoustic attractants. Lures provoking repulsion in one or more target species are not good candidates to be included in multispecies monitoring protocols. Using visual or auditory devices similar to the ones we tried may not be justified for multispecies monitoring of Iberian mammals. In contrast, detections were similar regardless the type of scent used, suggesting that none of the scents we employed caused apparent aversion relative to each other in any of the species we could examine.

Seasonal differences in indicators of lure performance were only apparent for some species. For them, detection, LTD, and POD in spring (the warmer season in our study area) were invariably lower than in autumn. These results do not support the hypothesis that diffusion of scents was enhanced at high ambient temperatures inducing a more efficient attraction. Indeed, as olfactory attractants are highly volatile (Roughton and Sweeny 1982), in the warm season they could completely evaporate soon after deployment or refreshment, causing a quick decrease in attraction. Besides, our study design did not allow separating the effects of scent height and detection method. However, for most species

detection frequency in plots with cameras and raised scents was lower than in scent stations where the attractant was placed on the ground (author's unpublished data), suggesting that positive effects, if any, of raising scents on detection through a better diffusion might be small, as we correctly assumed.

The interaction between the type of lure combination and covariates (cover, wind speed and moon illumination) was not significant for most species or attributes of attraction, suggesting that lure visibility did not play a role in the poor performance of plots equipped with visual or auditory lures. Again this indirectly points out to the hypothesis of aversion to novel structures. The reduced probability of detection of the European rabbit in dense cover could reflect habitat avoidance related with increased predation risk (Moreno et al. 1996) only if the effect was consistently found in all plots, but this explanation weakens because the relationship appeared only in plots with visual lures.

In large-scale multispecies monitoring, time and money are relevant factors. Suitable attractants should be easy to set and maintain and, ideally, should lure all mammal species occurring in the surveyed region (Paull et al. 2011). This may not be an easy task. For example, Monterroso et al. (2011) did not identify a single effective attractant for Iberian carnivore species; they had to combine two scents to effectively lure the seven species considered in their experiment. We detected all mammal species known to occur in at least one sampling unit, provided that they use the habitats where sampling plots were placed. However, we obtained very few records for six species after substantial effort. Ascertaining whether species detected with low frequency simply occur at low densities or are little interested in scents requires further study. Species detected with low frequency might have been missed by reducing the number of sessions or the spatial extent of our survey. Considering a plausible scenario of limited resources for conducting mammal monitoring across large areas, most survey designs might favour spatial replication to the detriment of temporal replication. This trade-off suggests that in many practical situations it may be unlikely that surveys will plan more than one or two sessions. Under these circumstances, when the principal aim of monitoring protocols is just detecting species

occurrence, the scents we used could reasonably satisfy the requirements for large-scale multispecies surveys for five common mammal species. Whether scents are also efficient for five additional species that were absent or scarce in our study area or the habitats we sampled (wildcat, stone marten, European polecat, Iberian lynx and Eurasian otter) awaits confirmation. Finally, FAS and catnip apparently show little promise as efficient attractants for the Eurasian badger, red deer and wild boar. Poor effectiveness in detecting some species also compromises the potential for using these scents as the only attractants for monitoring the whole community of Iberian larger mammals in Mediterranean environments.

For practitioners willing to use lures in their mammal surveys, we recommend FAS disks as a general-purpose attractant for the five mammal species subject to analysis because (i) their overall detection rate was slightly higher than that of catnip, (ii) it is a synthetic product and its formulation and presentation is repeatable, reducing potential effects on mammal response of variation in the chemical composition of natural substances (e.g., baits, urine or distilled essential oils as catnip), and contributing to a better standardisation of the monitoring protocols, (iii) it requires less handling time in the field because the plaster disk is already saturated with scent, and (iv) it is cheaper than catnip.

The use of multiple lures does not necessarily improve detection rates and simple scents may work as a generic attractant potentially useful for monitoring of mammal communities. Parallel to the efforts for searching specific lures for single target species, further study should be directed to find general-purpose lures that facilitate the simultaneous survey of several mammal species in other environments.

4.2 Relative efficiency of different survey methods for detecting wild mammals

Sign surveys have been broadly employed for monitoring mammal species (Kendall et al. 1992; Karanth et al. 2011) because they are relatively cheap and do not require animals to be directly observed or handled (Thorn et al. 2010). The performance of sign surveys usually depends on surveyor experience, ground and meteorological conditions, and species characteristics (Davison et al. 2002; Silveira et al. 2003; Gompper et al. 2006; Monterroso et al. 2013). Therefore, alternative passive methods, such as scent stations and camera traps, have been favoured for surveying mammals due to their effectiveness under multiple environmental conditions (Silveira et al. 2003; Barea-Azcón et al. 2007; McCallum 2013).

Using different measurements of performance, we found that, among the four techniques compared in this study, track surveys were the most efficient method for detecting wild mammal species in a Mediterranean environment. In contrast, the relatively low efficiency of passive methods was notable, taking into account that camera traps and scent stations are widespread methods for monitoring mammal species (Reed 2011; Paull et al. 2012; Monterroso et al. 2014). Indeed, camera-trapping was the least efficient survey method for detecting wild mammals. The poor performance of camera-trapping for detecting mammals in Mediterranean ecosystems was also reported by Barea-Azcón et al. (2007). In our study, the low efficiency of cameras might be partly due to difficulties associated with pressure-plate triggering systems (York et al. 2001). Current devices with motion activation systems and infrared night vision may provide higher detection rates, as suggested by the increasing number of investigations employing camera-trapping (Rowcliffe and Carbone 2008) but, to our knowledge, cameras are assumed to detect wild mammals more efficiently than sign surveys in most conditions without proper testing. Some authors pointed out that the elevated cost of cameras prompts the use of sign surveys or

other cheaper and equally effective survey methods, especially in large-scale multi-species surveys (Thorn et al. 2010).

Some mammal species can be very conspicuous, whereas others may be relatively difficult to detect, independently of the survey method employed. Detectability is often related to species density, daily movements and breeding cycle (Dempsey et al. 2014; Keeping and Pelletier 2014). Assuming that the variation in detectability attributed to species characteristics was similar among the different survey methods employed, we could assess their relative efficiency. As some species were detected exclusively by active methods, passive methods yielded many false negatives. Indeed, only track surveys detected all target species. Although track surveys recorded more species than scat surveys, the Eurasian otter and the stone marten were more likely to be detected by scat surveys, in agreement with previous findings (Barea-Azcón et al. 2007; Romanowski 2013). Therefore, recording both tracks and scats during the same field searches implies no additional effort, and may be advisable.

Uncertainty related to false negatives is a critical source of sampling bias in wildlife surveys, which can reduce the utility of monitoring programs (Reid et al. 2013; Santos et al. 2015). These biases are usually managed by implementing further statistical analyses or refining sampling designs (Tyre et al. 2003; Royle and Link 2006; Hamel et al. 2013; Guillera-Arroita et al. 2017). Due to pros and cons described for the different types of survey methods employed for detecting wild mammals, refinement of sampling designs usually includes multiple alternative survey methods to avoid false negatives (Li et al. 2012; Swan et al. 2014; Velli et al. 2015). However, monitoring programs seek to minimise sampling effort while maintaining a high probability of detecting biologically significant changes in abundance, distribution and connectivity (Travaini et al. 2010; Gormley et al. 2011; Powney et al. 2011). Therefore, the identification of a single cost-effective survey method will optimise sampling effort in monitoring programs without compromising data quality (Wright et al. 2014; Carreras-Duro et al. 2016). Here, we suggest the use of track surveys as a single cost-effective

method for detecting wild mammals in Mediterranean ecosystems with a habitat structure similar to those that we surveyed.

Our findings indicate that the combined use of scent stations, camera traps, track surveys and scat surveys was an effective strategy for detecting most, if not all, wild mammal species occurring in a region. However, the application of track surveys as a single cost-effective method was efficient enough to detect mammal species of interest at a low cost and with reduced searching effort. In both research and management, mammal surveys should ideally be quick and effective. Despite the rise in non-invasive genetic techniques (Steyer et al. 2013; Balestrieri et al. 2016) we conclude that simple track surveys could optimise sampling effort in monitoring programs and, under certain conditions (e. g., very large regions to survey) may be a suitable alternative to describe the dynamics of mammal communities in Mediterranean ecosystems.

4.3 Identification of critical connectivity routes for mesocarnivores across a Mediterranean agroecosystem

Connectivity has been traditionally measured by analysing landscape structure. A more realistic approach for measuring landscape connectivity also takes into account the behaviour of species, in term of movement patterns and habitat selection (Chardon et al. 2003; Revilla et al. 2004). The capacity to cross less suitable habitats during dispersal is intrinsically related to species-specific characteristics, as body size, habitat requirements, and behaviour (Uezu et al. 2005). As it is difficult to define which of these characteristics predispose a species to cross an unsuitable habitat, we simulated 27 different scenarios assuming different animal responses to local habitat quality and landscape configuration. Modifying the assumptions about how local habitat quality is perceived by carnivores and how the texture of resistances guides carnivore movement affected very little the placement of major routes of movement

across the agricultural landscape, suggesting that the amount of suitable habitat left and its spatial configuration might be the major driver of functional connectivity.

Our measures of functional connectivity for carnivores based on ecological species-specific habitat suitability for dispersal and potential responses to landscape configuration indicate 1) a high connectivity between forest and scrubland patches and numerous alternative dispersal routes within forest landscapes; and 2) low connectivity levels between forest landscapes due to the existence of a relatively broad and homogeneous fringe of agricultural land in the northern half of the intervening agroecosystem. The existence of multiple alternative paths within the forest landscapes shows, in general, a continuum of suitable habitats for dispersal, although land use transformation associated with forestry (mainly *Eucalyptus spp* plantations), agriculture and urban development partly constrain movement inside forest landscapes.

We only found three alternative dispersal routes connecting the forest landscapes across the agricultural landscape. Two of these pathways were identified near the arbitrary agroecosystem boundaries we set, whereas the pathways crossing the central region of the agroecosystem was predicted to be used with very low frequency. Large tracks of continuous open land would be avoided regardless the set of assumptions about friction we considered. A few kilometres of agricultural fields seem to work as an unsuitable barrier to carnivore movement. On the other hand, routes concentrated along heterogeneous areas composed of riparian, shrubland and forest patches. Hence, whereas matrix heterogeneity favours functional connectivity within forest landscapes, matrix homogeneity hinders functional connectivity within the agroecosystem (Baum et al. 2004; Revilla et al. 2004). These results support the hypothesis that considers the agroecosystem as a functional barrier for carnivore dispersal and demographic flow between forest landscapes.

The placement of connectivity routes was notably robust to variation in animal behaviour and species identity. We also performed a sensitivity analysis to explore the effect of the absolute values of friction, their range and the spacing between values to characterise differences in habitat preference (Suárez-Tangil and Rodríguez, unpubl.) and found almost no changes in the identification and placement of least-cost paths and bottlenecks. A single least-cost path may not predict reliably or accurately the location of animal movements (Pullinger and Johnson 2010). The use of multiple scenarios, fed with realistic up-to-date behavioural information for multiple species, may be more valuable and accurate than the information obtained from a single least-cost corridor to predict biologically meaningful locations of important connectivity routes (Sawyer et al. 2011).

Critical connectivity sites

The identification of landscape elements that may potentially increase or decrease connectivity between natural areas is an important task in planning and implementing conservation and restoration priorities (Rabinowitz and Zeller 2010; McRae et al. 2012; Kanagaraj et al. 2013; Martinez Pardo et al. 2017; McClure et al. 2017). We identified four critical connectivity sites within the agroecosystem that concentrated a high number of pathways between the forest landscapes. Sites were mainly characterised by coniferous and oak forests, riparian vegetation and scrubland patches. (Barros et al. 2016) found that the genetic diversity of Egyptian mongoose populations was related to dense shrub cover, and argued that the preservation of patches of Mediterranean scrubland benefits dispersal. Carvalho et al. (2016) found that common genets moved primarily within forest patches, close to riparian habitats, and avoided areas with a high road density. Santos et al. (2016) found that the occurrence of Mediterranean carnivores in riparian habitats was significantly higher than away from them, suggesting their use as a tool for

improving connectivity in fragmented landscapes. These results emphasise the validity of the friction values assigned in this work, reinforcing the confidence in our simulations.

The identification of only four critical connectivity sites along the two major dispersal pathways remarks the importance of their conservation to preserve connectivity across the agricultural landscape (Zelnik et al. 2015). Indeed, the loss of these sites could increase the isolation and, therefore, decrease genetic and demographic flow between forest landscapes (Newmark 2008; Lees and Peres 2009; Laurance et al. 2012). Hence, we stress the importance of knowing and understanding the habitat selection during carnivore dispersal to provide more realistic and reliable connectivity models for ecological investigations.

Connectivity restoration

In places where the restoration of large habitat patches is not possible, as in intensive agricultural landscapes, the recreation of linear elements made of woody plants is a useful alternative (Benton et al. 2003; Lawson et al. 2014). Červinka et al. (2013) identified several characteristics that make such "corridors" suitable for carnivores, namely prey availability, corridor width, the proportion of woody cover and absence of roads with high traffic. As the establishment of corridors between habitat areas can be costly (Dennis et al. 2013), the use of man-made physical structures and existing natural elements may be a potential solution (Magioli et al. 2016). One alternative is the use of woody linear elements in the boundaries of agricultural fields such as hedgerows. Hedgerows are important for biodiversity conservation (Wehling and Diekmann 2009; Sullivan et al. 2012) and the maintenance of ecosystem services (Dainese et al. 2017). Some species use hedgerows as movement conduits (Davies and Pullin 2007). Dondina et al. (2016) described the importance of a complex physical structure dominated by the shrub layer to

manage hedgerows as effective ecological corridors for mammals, whereas Pereira and Rodríguez (2010) reported that carnivores were able to establish a continuous population, with adjacent home ranges, in a landscape containing < 5% of suitable habitat. Therefore, the use of a cheap and efficient alternative to the creation of large forested patches should be taken into account for connectivity restoration within agricultural landscapes. Our simulations suggest that restoration of hedgerows in areas where the agroecosystem narrows, would promote the creation of alternative dispersal paths, what could increase connectivity between forest landscapes for the wildcat. This kind of strategies aiming to reduce resistance will help improve landscape connectivity (Ricketts 2001). However, improvement might depend on the restoration effort: increasing the size of the restored hedgerow and the number of hedgerows restored within the agroecosystem, restoration should also be effective in areas where the agroecosystem becomes wider.

Management implications

Recent advances in landscape connectivity are associated with experimental studies based on genetic information or individual-based dispersal behaviour (Carvalho et al. 2016; Poniatowski et al. 2016). Nevertheless, experimental studies on dispersal are usually time-consuming and expensive, especially in large areas and in species with low-density population, as carnivores (Kindlmann and Burel 2008; Kanagaraj et al. 2013). Least cost paths have been described as measurements that represent species dispersal more effectively than Euclidean distances (Driezen et al. 2007; Magle et al. 2009), providing better instruments for conservation management decisions (Mühlner et al. 2010). Hence, although least-cost models are not as accurate as other methods to assess functional connectivity (Reed et al. 2017), they offer an estimation of landscape connectivity for a group of species when little field data information is available (Zeller et al. 2012).

The agricultural intensification occurring in Mediterranean ecosystems, especially in plain and coastal areas, have partly contributed to habitat loss and fragmentation (Serra et al. 2008; Gobinda Roy et al. 2015) which, in turn, also reduce biodiversity (Santos et al. 2002; Virgós et al. 2002; Mortelliti et al. 2010). We suggest that conservation strategies should be oriented to preserve critical connectivity sites identified across the agroecosystem. The loss of these sites could represent the isolation of the forest landscapes which, in turn, would promote a decrease in the demographic and genetic flow. Additionally, restoration strategies to reduce movement resistance will help improve connectivity. Hence, we also suggest that the restoration of hedgerows around agricultural fields within the agroecosystem will improve connectivity between forest landscapes.

4.4 The influence of landscape heterogeneity on carnivore occupancy of forest fragments in a Mediterranean agroecosystem

Agricultural intensification leads to the loss of ecological heterogeneity at multiple spatial and temporal scales (Benton et al. 2003; Geri et al. 2010), which might also affect species occupancy in remnant fragments. Carnivore incidence in the study area was simultaneously affected by fragment quality, landscape context and regional connectivity variables. These landscape variables represent processes occurring at different spatial scales. Whereas landscape context and regional connectivity variables focus on the species movement among fragments, fragment size and quality are associated with the species settlement in those habitat remnants (Baguette et al. 2013). In our study, regional processes, represented by landscape connectivity, contributed to explain a substantial fraction of variation in fragment occupancy for some species.

We identified two different landscapes within our Mediterranean agroecosystem: a functionally continuous, mosaic landscape with relatively low

resistance to movement, and a functionally discontinuous, simplified landscape with relatively high resistance to movement. Fragment occupancy of these landscapes was associated with different ecological processes. In the mosaic landscape, movement between fragments is enhanced (Prevedello and Vieira 2010), and individuals are allowed to choose suitable fragments or groups or nearby fragments for settlement. Conversely, in the simplified landscape remnant fragments might have a lower probability of being occupied because movement across the landscape might be diminished (Magrach et al. 2012), limiting (re)colonization and rescue effects (Mönkkönen et al. 2014). Therefore, species seem to occupy well-connected fragments within the network, prioritising connectivity among habitat fragments rather than fragment quality. Thus, the relative contribution of fragment quality, landscape context and regional connectivity depends on the agroecosystem internal heterogeneity and, ultimately, on the proportion of forest left.

Our results support this hypothesis for the Eurasian badger and the Egyptian mongoose: in fragments located in the simplified landscape, landscape context and regional connectivity explained more variance than in fragments located in the mosaic landscape. Therefore, as woody cover decreases, the contribution of landscape context and regional connectivity variables increases. Nevertheless, the occupancy of the common genet occupancy was mostly determined by fragment quality, and the contribution of local landscape context and regional connectivity variables in the simplified landscape was lower than in the mosaic landscape. In the simplified landscape, where habitat amount is low and landscape resistance is high, Eurasian badger and Egyptian mongoose occupied less functionally isolated fragments, that is, fragments were not only well connected locally but also suitably placed within the fragment network. Thus, landscape context and regional connectivity might promote the (re)colonization and rescue effect from other occupied fragments (Borges-Matos et al. 2016), contributing more to fragment occupancy than in areas where habitat amount is not as reduced. However, in the case of the common genet, this hypothesis was

not supported because the contribution of landscape context and regional connectivity decreased as the percentage of forest in the landscape decreased. In the simplified landscape, the common genet seems to use fragments with especially favourable habitat conditions instead of well-connected fragments. The persistence of the common genet in the simplified landscape might be due to rare events of migration from the mosaic landscape (Zelnik et al. 2015), 2) a combination of locally favourable environmental conditions and 3) lasting establishment of one or a few breeding individuals in the larger fragments.

Species-specific responses to habitat quality and surrounding landscape (Uezu et al. 2005; Mendes et al. 2017) as well as species-specific differences in dispersal ability, should account for the patterns of fragment occupancy. Nevertheless, in the mosaic landscape, where habitat amount is high and landscape resistance is low, we find a similar response across species. Occupancy of the three carnivores appeared to be mostly determined by fragment quality. We suggest that in the mosaic landscape the movement between habitat fragments has a very small cost and animals would easily go everywhere. Therefore, as in an ideal free distribution model (Fretwell and Lucas 1970), carnivores might choose the most suitable local conditions (Fahrig 2007; Pereira and Rodríguez 2010).

We found support for our hypothesis that regional connectivity adds valuable information to fragment quality and landscape context alone, by capturing additional ecological processes and providing insight into patterns of fragment occupancy. Further, the identification of homogeneous landscapes within the heterogeneous agroecosystem helped to tell different patterns of occupancy possibly related to different ecological processes, which would go unnoticed if the whole agroecosystem would have been analysed as a homogeneous entity. This has important implications for wildlife management because different conservation strategies should be applied depending on the landscape heterogeneity. Thus, depending on the amount of habitat within the agroecosystem, conservation measures should focus on a) the conservation or restoration of transformed or degraded fragments in mosaic landscapes; and b)

the conservation or restoration of fragments placed in specific locations that enhance connectivity of the fragment network in simplified landscapes.

4.5 Regional and local processes of mesocarnivore community assembly in an agroecosystem surrounded by Mediterranean forest

The regional mesocarnivore species pool was fully represented in Sierra Morena, whereas the agroecosystem and the Doñana forest landscape contained only a subset of species. These differences in community composition are in agreement with the hypothesis that carnivore local communities become progressively impoverished in a gradient of anthropic pressure. Global and regional patterns of decreasing richness associated to human activities have been described elsewhere (Attwood et al. 2008; Gibbs et al. 2009; Newbold et al. 2015; Bogoni et al. 2016). However, there is little information available about the relative contribution of specific regional and local factors to variation in species composition (da Silva and Medina Hernández 2014; Heino et al. 2017; Trivellone et al. 2017), especially for carnivores. Our work provides the first quantitative analysis of dissimilarity components in carnivore metacommunities.

Contrary to what we expected, the turnover dissimilarity component was more important for total dissimilarity than the nestedness component. Therefore, despite the nested pattern of species composition between landscapes, most of the variation in local species composition was related to species replacement. These results resemble the relative importance of the turnover dissimilarity component along a latitudinal pattern, with a high contribution at low latitudes and a low contribution at high latitudes (Soininen et al. 2018). This pattern might be related to the higher environmental heterogeneity found at low latitudes: the more heterogeneous the environment, the higher the turnover dissimilarity

component. In our study, species-specific responses to complex Mediterranean landscapes may increase the contribution of the species replacement for explaining the total variation in species composition (Herrera et al. 2016).

Regarding the nestedness dissimilarity component, the hypothesis of dispersal limitation could be plausible considering the high resistance of the northern part of the agroecosystem for the movement of carnivores but receives little support from the regional patterns of dissimilarity. The comparison between species-specific dispersal distances was incoherent with mesocarnivore distribution across the study area. This suggests a negligible effect of dispersal ability on the nestedness component and perhaps also a relevant effect of unmeasured environmental variables. However, the joint effect of spatial structures and environmental variables contributed more than pure spatial and pure environmental variables for explaining variation in mesocarnivore species composition. This often results because of the simultaneous effect of environmental variables and spatial structures (Heino 2011; Leroy et al. 2013) on local (i. e., habitat filtering) and landscape (i. e., dispersal limitation or unmeasured environmental variables) spatial extents. For example, the individual contribution of the relative proportion of scrubland to explain variation in species composition was partly due to its role as a local habitat variable but also because it was spatially autocorrelated. Indeed, the spatial pattern of the shrubland cover within the sampling units explains the variation in mesocarnivore species composition attributable to a spatial pattern of species loss, in which the most human-altered sites (i. e., sites with a low proportion of shrubland), are only inhabited by a similar subset of species, while species with a lower tolerance to changes in local and landscape conditions are absent (Curveira-Santos et al. 2017). Shrubland cover has been previously described as a positive predictor of carnivore occurrence in farmlands (Červinka et al. 2013), especially in Mediterranean areas (Mangas et al. 2008; Pereira and Rodríguez 2010). Carnivores seem to find essential resources such as prey and refuge in this shrubland patches (Pereira and Rodríguez 2010). In our study area, the

relative proportion of shrubland decreased drastically from Sierra Morena to the Guadiamar agroecosystem, which is consistent with the pattern of species loss from richer communities.

Most of the total dissimilarity was due to species replacement, which is likely to be associated with habitat filtering processes in our study area and elsewhere (Liu et al. 2015; Gianuca et al. 2017). The simultaneous gain and loss of species among local communities was exclusively related to the combination of local and landscape environmental variables. Specifically, the mean proportion of open habitats at the local scale and tree cover at the landscape scale explained two-thirds of the variation in species composition. Mesocarnivore species usually select a combination of mosaics and complex multilayer habitats with cover at both the understorey and the canopy levels (Palomares and Delibes 1993; López-Martin et al. 1998; Rondinini and Boitani 2002; Lozano et al. 2003; Palomo et al. 2007; Rosalino et al. 2008; Galantinho and Mira 2009; Lozano 2010; Recio and Virgós 2010; Sarmento et al. 2010; Cruz et al. 2015). The proportion of open habitat and the homogeneous stands of pine and oak wood plantations could help to filter the establishment of certain species (Suárez-Tangil and Rodríguez, unpublished).

The variation in species composition between sites can also be a consequence of ecological interactions (Azeria et al. 2012; Colorado and Rodewald 2015; Camarota et al. 2016). Although some authors have reported aggregated patterns of carnivore co-occurrences in agricultural landscapes (Šálek et al. 2014), underlying processes such as changes in species composition driven by species-specific dispersal abilities often cannot be distinguished from responses to environmental quality (Ulrich and Gotelli 2013). We found a marked trend toward segregation in carnivore co-occurrence. In Mediterranean landscapes, overlaps in patterns of diet and activity in mesocarnivore species depends on resource availability (Barrull et al. 2014) or temporal segregation in resource exploitation (Barrientos and Virgós 2006). Indeed, species coexistence can be promoted by the fine-scale spatiotemporal segregation (Fedriani et al. 1999;

Mangas et al. 2007; Viota et al. 2012), even in homogeneous landscapes (Soto and Palomares 2015). Local communities might reflect competitive exclusion in terms of exploitative competition for resources (Camarota et al. 2016; de Satgé et al. 2017) or interference competition (Wolsan 1993; Sunquist and Sunquist 2002; Moleón and Gil-Sánchez 2003). As no records of competitive exclusion between our study species have been described so far, we suggest that the effect of the spatial segregation on the variation in species composition may be negligible in comparison to other local and regional processes. Nevertheless, we stress that interspecific interactions might contribute to determine species composition, so in-depth investigation of interspecific interactions is needed before discarding their contribution to community structure assembly.

So far, the role of local and regional processes as determinants of local species composition has been mainly studied in aquatic environments (Soininen et al. 2018). Mammals (and especially carnivores) have been examined very rarely (Bogoni et al. 2016). In a fragmented Mediterranean agroecosystem, we found different processes affecting variation in mesocarnivore species composition. These processes were principally associated with species replacement, whereas the spatial pattern of species loss only represented a small part of the variation in species composition. We conclude that turnover dissimilarity was the principal driver of carnivore community structure, explained by a species-specific habitat filter, little influence of species-specific dispersal ability, and maybe a role for interspecific interactions between mesocarnivores that deserve further investigation.

4.6 General implications

With this study we contribute with new information about the simultaneous local and regional processes affecting carnivore species in a restored Mediterranean fragmented agroecosystem. This thesis highlights the role of

regional processes shaping mesocarnivore occupancy patterns and metacommunity structure, emphasizes the importance of landscape perception for measuring functional connectivity, and underlines the efficiency of specific monitoring tools in multiple-species large-scale studies.

Ecologists analysing the dispersal and environmental effects on the metacommunity structure have mainly focused on aquatic invertebrates (Soininen et al. 2018). However, the structure of carnivore communities has traditionally been explained by species-specific responses to a combination of local and landscapes factors (Jennings et al. 2015; Gompper et al. 2016; Curveira-Santos et al. 2017). Very few works have attempted to tackle the simultaneous effect of regional, landscape and local processes on carnivore species composition (Bogoni et al. 2016). This study contributes to expand the general knowledge about how explicitly defined variables representing regional and local processes affect mesocarnivores at both species and community levels, and analyse the relative contribution of these processes on the mesocarnivore distribution across a restored Mediterranean fragmented agroecosystem.

Least-cost models have been broadly applied for designing corridors (Beier et al. 2009; De La Fuente et al. 2018) and describing potential dispersal routes for organisms (LaRue and Nielsen 2008; Li et al. 2010). Nevertheless, they have been criticised due to their lack of realisms (Crooks and Sanjayan 2006). This thesis focuses on species perception of the landscape structure by accounting for different factors that are expected to affect species movement across the agroecosystem. We improve the general knowledge about how least-cost models can help assessing functional connectivity for carnivores in fragmented landscapes.

Most research on lure and survey methods efficiency has pursued optimising detection of particular species while trying to keep low visitation rates by non-target species (Travaini et al. 2001; Schmidt and Kowalczyk 2006). In contrast, comparison and selection of lures to simultaneously monitor multiple mammal

species have drawn less attention. In this study, we also contribute new information on the effectiveness of mammal monitoring tools and their applicability on multiple-species large-scale studies.

We analysed the efficiency of olfactory, visual and acoustic lures in detecting mammal species throughout the agroecosystem, observing that fatty acid scent disks are an efficient general-purpose attractant. We also evaluated the effectiveness of passive and active survey methods in detecting mammals, finding that track surveys are efficient enough to detect mammal species of interest at low cost and reduced searching effort. We also estimated carnivore connectivity routes between forest landscapes across the agroecosystem, observing that simulated landscape perception in least-cost models provided only a few alternative connectivity routes in which several critical connectivity bottlenecks. Hedgerow restoration could increase connectivity throughout the agroecosystem. The inclusion of variables associated with regional processes provided a more accurate insight into the assessment of the ecological processes determining species distribution in fragmented agroecosystems. Further, the relative contribution of regional and local processes on fragment occupancy by species varied with landscape internal heterogeneity. Mesocarnivore metacommunity structure was primarily characterised by changes in species identity between communities. The species replacement was mostly explained by species-specific habitat filters, although species interactions may also play a minor role in carnivore assembly. We also identified a spatial pattern of species loss associated to spatially autocorrelated habitat conditions.

Monitoring Iberian mammals

There is a wealth of scientific literature evaluating the efficiency of lures for detecting particular mammal species of interest (McDaniel et al. 2000; Spurr et al. 2004; Hunt et al. 2007). This is not different in the case of Iberian mammals,

where different lures and combinations of different attractants have been employed to optimise the detectability of certain species (Garrote et al. 2012). Only a few studies have analysed the effectiveness of a single cost-effective lure for detecting several mammal species (Andelt and Woolley 1996; Read et al. 2015). However, only the combination of different lures has provided positive results in detecting several mammal species (Monterroso et al. 2011). In large-scale multispecies monitoring, time and money are relevant factors. Suitable attractants should be easy to set and maintain and, ideally, should lure all mammal species occurring in the surveyed region (Paull et al. 2011). We focused on finding a single cost-effective lure that allows the detection of all mammals occurring in a large region. We find that fatty acid scent disks are cost-efficient lures for detecting at least five Iberian mammal species, which could promote less expensive monitoring programs at a large scale in Mediterranean ecosystems.

Assessing the efficiency of survey methods for detecting wild mammals (Silveira et al. 2003; Garden et al. 2007; Long et al. 2008) has been another goal of this thesis. As attractants, for the sake of the monitoring economy and efficiency, survey methods should ideally detect every species occurring in an area. In recent years, camera-trapping has become a standard survey method for detecting wild mammals, especially cryptic species with elusive behaviour (Trolle and Kéry 2005; Pettorelli et al. 2010; Stokeld et al. 2015). However, in large-scale monitoring programs, the use of cameras may be impractical because of their cost and technical performance. We find that the use of sign surveys may become an effective alternative in monitoring programs at a large scale.

Functional connectivity in fragmented agroecosystems

Least-cost models have been employed in the recent years as a flexible tool to model landscape connectivity, relating landscape structure and the movement

capacity of organisms (Adriaensen et al. 2003). Indeed, multiple conservation programs have proposed the establishment of ecological corridors basing on least-cost models (Klar et al. 2012; Riggio and Caro 2017; De La Fuente et al. 2018). However, realistic least-cost models accounting for factors affecting animal movement or considering the effects of adjacent habitats are scarce (Sawyer et al. 2011). Therefore, we calculated least-cost paths for several mesocarnivore species in different scenarios accounting for a) landscape resistance between closer patches; b) patch size; and c) adjacent heterogeneity. Modifying the assumptions about how landscape structure is perceived by carnivores affected very little the placement of major routes of movement across the agricultural landscape, suggesting that the amount of suitable habitat left and its spatial configuration might be the major driver of functional connectivity. However, the use of multiple scenarios, fed with realistic up-to-date behavioural information for multiple species, may be more valuable and accurate than the information obtained from a single least-cost corridor to predict biologically meaningful locations of important connectivity routes (Sawyer et al. 2011) and identify areas in which restoration could increase connectivity.

Relative contribution of regional and local variables in determining mesocarnivore distribution in fragmented agroecosystems

At the species level, mesocarnivore distribution in fragmented landscapes is explained by a combination of the amount of suitable habitat left and landscape configuration (Virgós and García 2002; Mortelliti et al. 2012; Mendes et al. 2017). For simplicity, the matrix where habitat fragments are embedded is often considered of homogeneous quality, despite such quality should vary as the habitat quality of the fragment does (Prugh et al. 2008). In our study, regional processes, represented by landscape connectivity, contributed to explain a substantial fraction of variation in fragment occupancy for some species.

Accounting for different landscapes within our Mediterranean agroecosystem allowed as to find that the relative contribution of fragment quality, landscape context and regional connectivity depends on the agroecosystem internal heterogeneity and, ultimately, on the proportion of forest left. Further, although regional processes have gone unnoticed in previous occupancy models, it was especially important for explaining species occupancy in highly-transformed landscapes. This has important implications for wildlife management because, depending on the amount of habitat within the agroecosystem, conservation measures should focus on the conservation or restoration of transformed or degraded fragments in mosaic landscapes; and the conservation or restoration of fragments placed in specific locations that enhance connectivity of the fragment network in simplified landscapes.

At a community level, a large body of scientific literature has focused on explaining the relative contribution of regional and local variables on the variation in species composition between ecological communities (Pöyry et al. 2009; Grönroos et al. 2013; Heino 2013a). This question of general ecological interest is especially relevant in fragmented landscapes, where landscape heterogeneity may favour or impede the dispersion and settlement of the species, or even promote or limit interspecific interactions (Öckinger et al. 2012; Leavitt and Fitzgerald 2013; Rösch et al. 2013). Nevertheless, little is known about how regional and local variables influence variation in mesocarnivore species composition (Bogoni et al. 2016). This underrepresentation can have critical ecological implications because carnivores, characterised by their relatively large ranges and dispersal ability, broaden the perspective of metacommunity dynamics (Logue et al. 2011), a topic often studied in small aquatic invertebrates (Soininen et al. 2018). Variation in mesocarnivore species composition was mainly driven by changes in species identity (turnover dissimilarity), which is, in turn, related to interspecific interactions and the variation in local environmental conditions across the agroecosystem.

Future steps

This study explicitly defined variables representing regional and local processes affecting mesocarnivores in both species and community level, and analysed the relative contribution of these processes on carnivore distribution across landscapes with different degree of anthropogenic pressure. On the one hand, we provide more comprehensive results on fragments occupancy, at the species level, by including variables associated with the regional connectivity existing within agroecosystems. We emphasized that the relative contribution of regional and local drivers of species occupancy depends on the internal agroecosystem heterogeneity. Additionally, we made some progress in studying which regional and local factors determine mesocarnivore assembly patterns in an agroecosystem surrounded by forest landscapes. We underline the importance of the simultaneous effect of species-specific habitat filters, interspecific-interactions and the effect of spatially autocorrelated habitat conditions for mesocarnivore metacommunity structure. We increased the functionality of least-cost models by assuming different criteria associated with the species perception of landscape structure in heterogeneous systems such as transformed agroecosystems. This is not only helpful for providing more robust inferences on landscape connectivity but also for identifying critical connectivity sites that could be relevant for mesocarnivore conservation in fragmented landscapes. Further, we propose that the restoration of linear hedgerows within the agroecosystem could increase connectivity between natural areas by creating alternative connectivity routes between them. Therefore, we improved the general knowledge about how landscape connectivity influences Mediterranean mesocarnivores in fragmented agroecosystems. Here, we also evaluated mammal monitoring tools, providing helpful recommendations for future mammal surveys in Mediterranean landscapes. These recommendations could be especially useful for both scientific investigations and mammal monitoring within conservation programs. Hence, we contributed to expand the general knowledge about different aspects affecting mammals monitoring and

conservation in Mediterranean fragmented agroecosystems. We contribute with new information on the effectiveness of mammal monitoring tools and their applicability in multiple-species large-scale studies.

To deal with future food demand, the productivity of agricultural landscapes is expected to increase, promoting changes in land use from wildlife-friendly farming to intensive cultivation. With this thesis, we offer new insights about how land use changes affect carnivores (at both species and community levels) in highly-transformed areas such as Mediterranean agroecosystems. We have shown that the agroecosystem structure and configuration negatively affect functional connectivity between forest landscapes, the distribution of species within the agroecosystem, and the metacommunity structure across the study area. However, we also discuss some strategies that could alleviate these negative effects. All this information might help managers and researchers to harmonise biodiversity conservation and competing demands for land exploitation in agricultural landscapes.

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